CHICK DEVELOPMENT AND PARENTAL CARE IN THE NORTHERN GANNET

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Chick Development and Parental Care in the Northern Gannet

by

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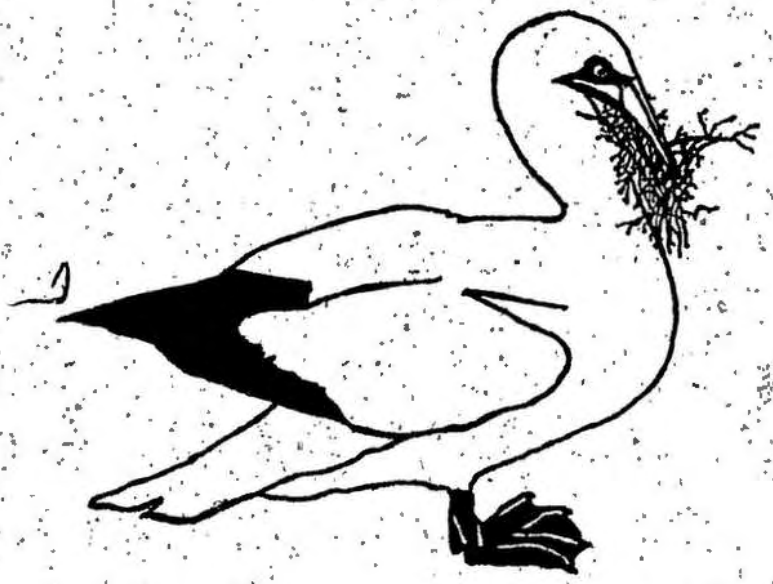

Abstract

Parent-young interactions in Northern Gannets (Morus bassanus) were studied at three North American colonies in 1978 and 1979. Nestling behavioural and morphological development were investigated using wild and hand-reared chicks. During the first month post-hatch, certain body parts grow faster than others. Rapid growth of tarsi, midtoes, culmen, and associated muscles aid in eventual thermoregulatory activities and in increasing the efficiency of food reception. Metabolic rate ($\dot{V}O2$) of nestlings between 5 and 10 days was high and variable and declined in magnitude and variability to near adult levels by 21 days. When endothermic, chicks had low metabolism and thermoregulation did not appear to require much of the available energy, most of which was allocated to growth.

Chick dependence on adults requires continuous attendance and care (brooding and feeding). Relative parental investments by males and females were determined by observation of time spent incubating, brooding, foraging and feeding chicks. Daily nest attendance by both parents was similar during egg and chick stages. Females incubated, on average, for significantly longer periods than males. Chick brooding and attendance spells were shared about equally by males and females. Males fed chicks more often than females, during post-hatch weeks 1 through 3; thereafter chick feeding was shared about equally between parents.

The food energy requirements of nestlings peaked at about week 6 and declined slightly after week 9. Mackerel,

which has a high fat content and caloric value, was the most common food fed to chicks. Mackerel is an ideal food type for gannets, because of its large size (fewer foraging trips) and its high levels of fat which nestlings require for post-fledging survival. The gannets' mode of development is discussed in terms of nestling behaviour and energetics, parental time and energy investments, and with comparisons to other avian development patterns.

Acknowledgements

I wish to express my gratitude to Dr. William Montevecchi whose investment in all stages of this study far exceeded that of parent gannets in both time and energy. Brian Harvey and Lee Grimmer helped with the field work in 1978 and 1979, respectively. Special thanks to Randy Purchase who participated in the field during both yesrs. Dr. Robert Ricklefs offered useful suggestions regarding the metabolism tests. The Canadian Coast Guard Service provided transporation to and from Funk Island and tbe Bird Rocks. The lightkeepers provided accommodation and warm hospitality on Baccalieu Island and the Bird Rocks. Discussions with the late Dr. Les Tuck provided stimulation and encouragement. Drs. Jake Rice and Deane Renouf, Ms. Shelley Browne and Mr. Gordon Kirkham offered criticisms of the manuscript. My examiners, Drs. Erica Dunn and Jon Lien, thoroughly reviewed the thesis. To all involved in the thesis work and writing, I am sincerely grateful. This study was supported by a Canadian Wildlife Service Student Scholarship, and a NSERC Grant (No.A-0687) awarded to Dr. Montevecchi.

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INTRODUCTION

The patterns of avian development are diverse and correspondingly, there are many forms of parental care and investment. Developmentally, different species have evolved a variety of adaptations that are imperative for survival. In different families of birds, many of these adaptations are seen in the degree of maturity at hatching. Based primarily on behavioural and anatomical maturation at hatching, development can be categorized into three classes: precocial, semi-precocial and altricial (Heinroth, 1922; Nice, 1962).

Altricial young hatch blind and naked. Most body parts are immature, and chicks are poikilothermic for a period much longer than those of the other two categories. Chicks are therefore dependent on parents for body heat and food until fledging. The lack of efficient temperature regulatory abilities by chicks necessitates parental brooding. Prey species are often located great distances from the nest site and require foraging skills of which only fledged individuals are capable. Examples are most passerines and gannets.

Developmental strategies are generally considered to be affected by internal physiological contreints in young, predation pressures, and the rates at which adults can deliver food energy to nestlings (Lack, 1968; Ricklefs, 1968a, 1979a). There are two basic components in the energy required for nestling growth: body maintenance and growth itself (Ricklefs, 1968a), and thermoregulation (Dunn, 1980).

As nestlings acquire a covering of down, deposit layers of fat and decrease the surface to volume ratio, thermoregulatory capabilities develop and metabolism gradually stabilizes. The conductance and shivering of nestlings, respectively, allows heat to be lost at high temperatures and produced at low ones (West, 1965).

When considering energy allocation in nestlings, the physiological processes are not easily teased apart. During a critical period prior to metabolic and endothermic stability, certain unfavourable environmental conditions cause energy to be expended for thermoregulation. If, for instance, chicks must increase metabolic rates during a drop in ambient temperature, a proportion of the energy available for growth may have to be reallocated into maintenance of body temperature. According to Dunn (1980), the caloric requirements of growth and of body maintenance need not be viewed as competing for the same energy resource. Dunn's evidence and Ricklef's enigma (1979a) is that some semi-precocial gulls and terns grow as rapidly as altricials of similar body despite the greater proportion of mature body parts and higher thermoregulatory costs found in the former. It appears that there are a limited number of patterns in which body parts grow relative to each other (see Figure 6 in Ricklefs, 1979a). Chicks unable to effectively thermoregulate are extremely vulnerable to temperature fluctuations in that growth and even survival

are affected in extreme circumstances. The acquisition of endothermy is an important transition in post-natal development, since the young animal achieves thermal independence from its parents.

Parental care and energy contributions to nestlings vary with mode of development. The period of thermal dependence of altricial young involves substantial time investment by parents in brooding and nest attendance. Adults of precocial species have a different investment pattern. Many precocial young are never fed by parents and are totally self-sufficient within hours of hatching. Parental investment is seen primarily in the aiding of nestlings in their search for food, and probably through protection from predators. Parents feed semi-precocial chicks, but often decrease their care or attention after chicks are homeothermic.

The evolution of altriciality, endothermy and parental care are thought to be all closely correlated (Hopson, 1973; Case, 1978a,b; Martin, 1980). Hopson (1973) feels that altriciality evolved (in mammals, with some avian parallels) to reduce the greater energetic requirements of endothermic young. If the onset of endothermy is delayed until some time later in the nestling stage, more of the energy provided by parents will be channelled into growth rather than body temperature maintenance. Thus, altricial development with delayed endothermy necessitates greater

parental behaviour and care. Case (1978a) points out that total energy savings for parents would be greater if more energy was put into the embryo (egg) and therefore less into the newborn, because it may be cheaper to invest heavily in eggs than offspring. However, if mortality is greatest during the egg stage, it may be cheaper to invest more into rearing chicks. The energy for egg production is gathered and expended over a short time, which when compared to the energy invested over the nestling period, may not necessarily be an energetically cheaper reproductive investment. Case notes that many of the foods eaten by birds and their methods of capturing it preclude the development of precocial young. In these instances, altriciality may be the favoured route. Gannets are specialized feeders, employing methods which only fully fledged and experienced birds can efficiently exploit. Since gannet (and other altricial) chicks have a peak energetic requirement sometime during the nestling period, parents must spend a greater portion of their time foraging compared to parents whose offspring develop more precocially.

Monogamy is favoured under the altricial conditions (Case, 1978a). It is worth noting that more than 80% of all bird species are altricial (Ar and Yom-Tov, 1978) and of all the passerines (the majority of which are altricial), about 95% are believed to have a monogamous mating system (Verner

and Willson, 1969). Since both precocial and altricial species protect young, Case feels that postnatal care evolved prior to altriciality. However, the delay of endothermy caused parental care to become refined and extended in altricial individuals. Case (1978a) differs from Hopson in contending that the evolution of smaller and altricial young was due to "the relatively large amount of nonthermogenic tissue formed during egg production would have imposed a serious energetic burden ..." for adults.

The approach of the present study has been to consider the parent-young interactions on a descriptive level by incorporating certain energetic concepts. The primary objectives of this study were examination of: 1) the developmental pattern of nestling growth, energy assimilation, and behavioural adaptations, and 2) the parental time and energy investment of Northern Gannets. Post-hatching parental investment by gannets is of special interest, because they invest so little in egg production (Ricklefs and Montevecchi, 1979), and because they are the largest altricial species considered in view of reproductive time and energy investment (see Dunn, 1975a). Nestling growth and the pattern of parental care are considered as interacting morphological, physiological and behavioural adaptations, the study of which may help elucidate the adaptive significance of altriciality in gannets.

MATERIALS AND METHODS

Study Animal

Northern Gannets (Morus bassanus Vieill.) are long-living, pelagic seabirds that are sexually monomorphic and apparently mate for life (Nelson, 1978a). In North America the breeding season extends from nest-site occupation in April, until colony departure in late October. Colonies are typically insular and inaccessible to terrestrial predators. A single egg is laid in a shallow nest on a cliff ledge or grassy slope above cliffs. During the non-breeding season, gannets spend most of their time at sea.

Gannets belong to the order Pelecaniformes, which is comprised of six families: frigate birds (5 species), cormorants (27 spp.), pelicans (8 spp.), tropicbirds (3 spp.), anhingas (4 spp.), and gannets and boobies (9 spp.). The gannet's nomenclature includes no less than eight generic names and a score of vernacular names. Most of the common names such as 'solan' were derived from 'gander or goose. With regard to generic nomenclature, the American Ornithologists' Union adopted the genus 'Morus', in 1907, in contrast to the British Ornithologists' Union's choice of 'Sula'. The designation of the genus Morus puts the three gannet species in a genus separate from the boobies (Sula). Nelson (1978b), however, prefers to consider the gannets as superspecies and places all the boobies and gannets in the

genus Sula.

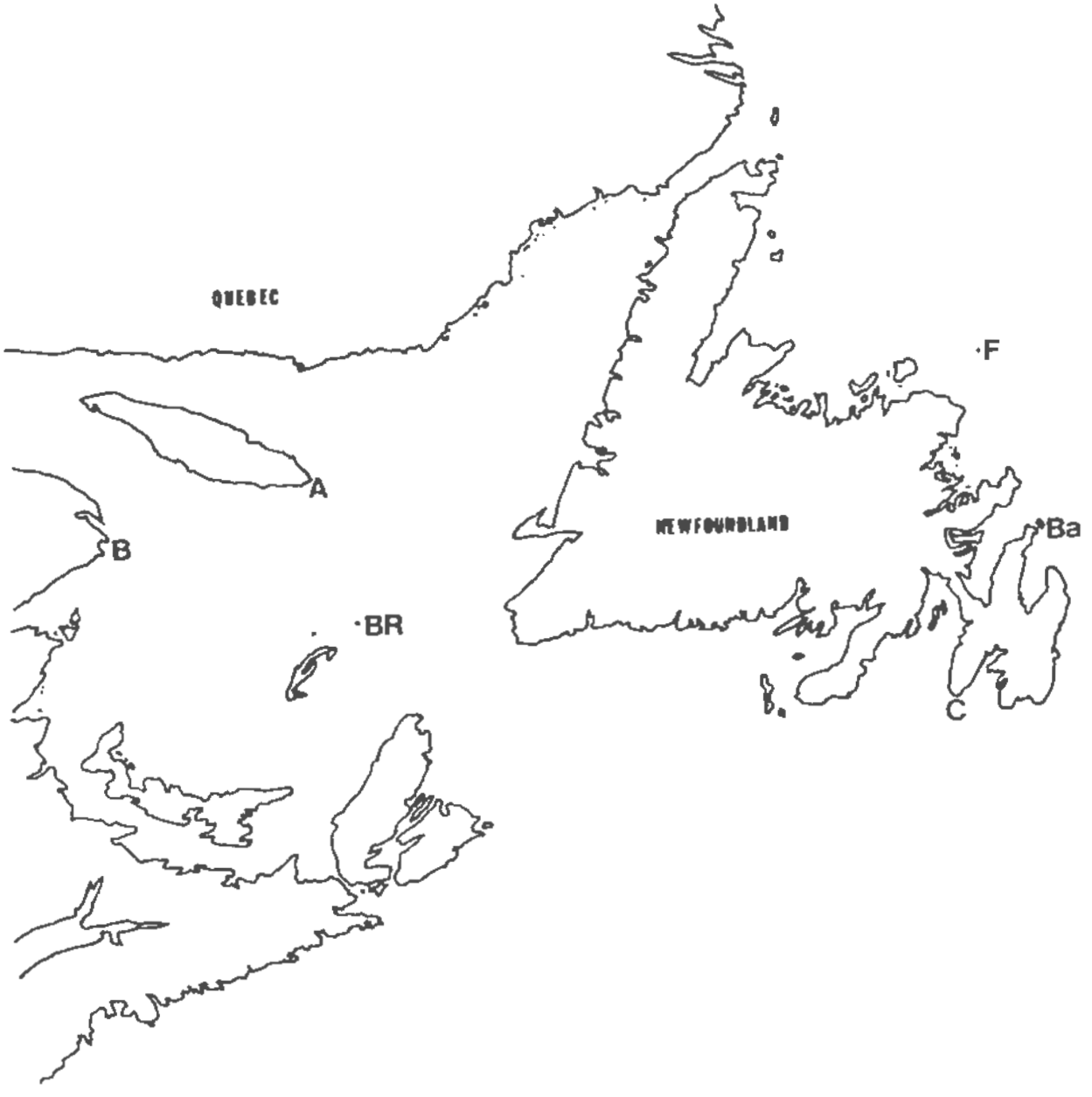
Study Sites

The study was carried out in three North American gannetries between May and August in 1978 and 1979 (Figure 1, see also Appendix A). 1) Great Bird Rock, Magdalen Islands, Quebec (47°50'N, 61° 09'W) is located near the geographic center of the Gulf of St. Lawrence. The top of the island is flat and grassy, oval in shape, about 0.4 km long by 0.1 km wide. The northern point is 43 m high, with a gradual downward slope to a height of about 26 m at the southern end (Nettleship, 1976). The sides are vertical and made up of a red sandstone. The light station on the island is still active and manned. A second and considerably smaller island, known as Little Bird Rock, is located about 1.2 km to the northwest across shoal water. It is conceivable that at one time the two rocks were one (Bryant, 1861).

2) Baccalieu Island, Newfoundland (48°07'N, 52°47'W) is located about 2.5 km north of the northwestern arm of the Avalon Peninsula, lying between Conception and Trinity Bays. The island is approximately 6.1 km long by 1.3 km wide. The gannetry is located on the eastern side on three vertical cliffs between 50 and 75 m in height (Montevecchi et al., 1980).

3) Funk Island, Newfoundland (49°46'N, 53°11'W) is a small granite rock situated about 56 km north-northeast from

Figure 1 - Map of North American gannetries: A-Anticosti Island, B-Bonaventure Island, BR-Bird Rocks, C-Cape St. Mary's, Ba-Baccalieu Island, F-Funk Island


QUEBEC
NEWFOUNDLAND
A
B
BR
F
Ba
C

Cape Freels. It is 0.8 km long by 0.4 km wide and is 14 m at the highest point (Nettleship, 1976). Gannets nest on the western end of the island. Additional descriptive reviews of these colonies can be found in Tuck (1961), Nettleship (1976), Nelson (1978a,b) and Montevecchi et al.(1980).

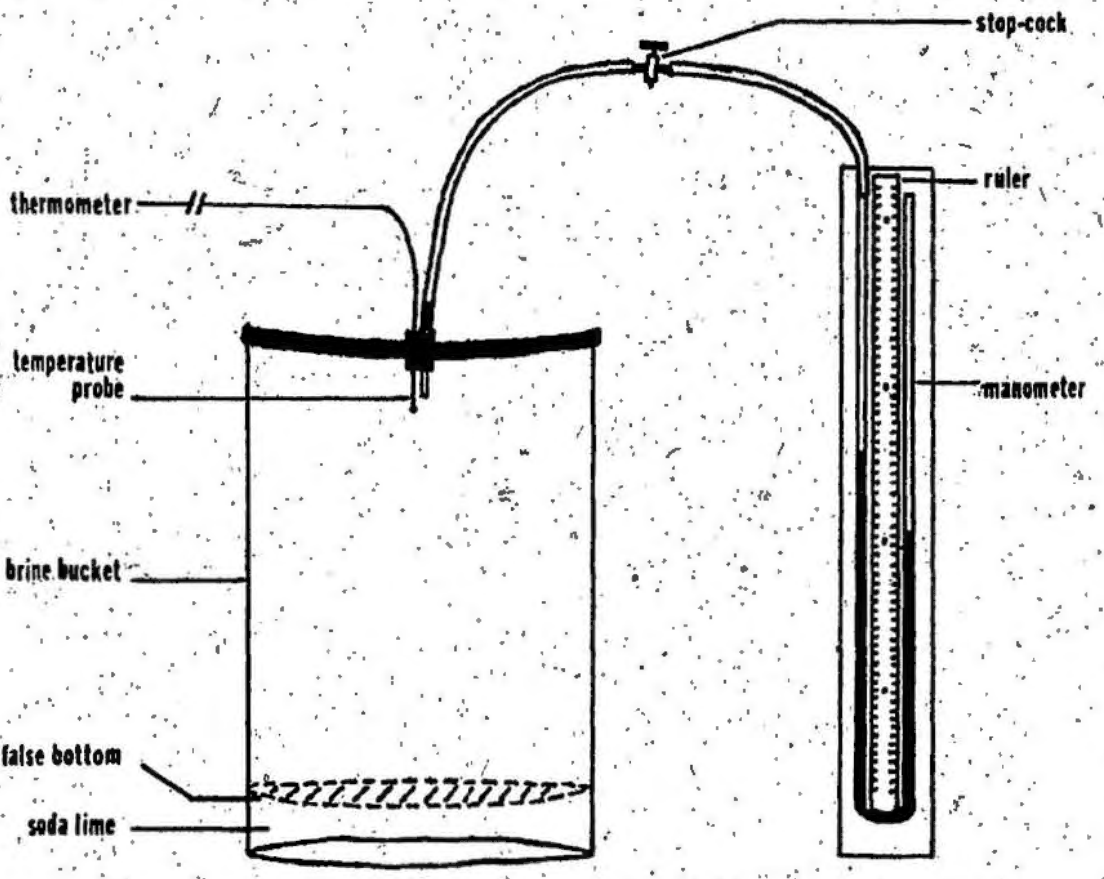
Data Collection

Chick growth measures are based largely on four chicks obtained on Baccalieu Island (two in 1978; two in 1979) within a week of known hatching dates. Captive chicks were fed capelin at frequent intervals (up to six times daily, or until satiated) for the first few weeks after hatching; chicks were then fed predominantly mackerel (two to three times daily, or until satiated); after two months, feeds were reduced to once a day. Feeds consisted of entire fish that were cut into pieces according to the size of chicks. Chicks older than eight weeks were given feeds of one-half a mackerel and occasionally an entire mackerel. Three of the captive chicks survived at least until fledging age and one died at 39 days. Weight increments of captive chicks were monitored on a regular basis throughout the nestling period (91 days), using Pesola spring scales (300, 500, 1000, and 5000 g) and were compared to those of other years (Nelson, 1964; Poulin, 1968). An additional comparison was based on the weight increments (n=57) on 15 chicks of known age from Great Bird Rock and Baccalieu Island, 1979. The following growth measurements were also recorded daily up to 21 days,

and every fifth day thereafter) from the captive chicks: 1) culmen (from tip of bill to base of feathers; n=48 measures), 2) wing (flattened, from tip of 10th primary to bend of folded wing; n=54), 3) tarsus (from behind middle-toe to heel of tarsus; n=23), and 4) middle-toe (from tip of nail to beginning of tarsus; n=42). An index of down growth was obtained by placing a 2.5 cm frame on the dorsal and ventral surface of chicks and estimating the percent cover. Photographs of the frame on chicks were taken other day from hatch to 3 weeks.

Rates of oxygen ($\dot{V}O_2$) consumption of wild chicks and adults were measured on Great Bird Rock and of chicks on Baccalieu Island. Two air-tight chambers were constructed from plastic brine buckets to accommodate chicks of various weights, and an additional chamber was made to accommodate fledglings and adults (see Figure 2). Chicks were tested in chambers according to age: 1-10 days, chamber volume = 4,615 ml; 11-21 days, chamber volume = 19,800 ml; adults, chamber volume = 59,400 ml. Chicks were probably not in a post-absorptive state during tests, as they were removed from nests usually in the morning and feeds often occur during early morning. Ambient temperatures (Ta) averaged ($\pm$SD) 28.4 $\pm$ 4.8°C and ranged from 17 to 35°C during tests, which is likely within the range of thermoneutrality for gannets. Standard test procedures included: 1) recording of cloacal temperature prior to and after testing, using a

Figure 2 - Diagram of oxygen consumption chamber.


stop-cock
ruler
thermometer
temperature probe
manometer
brine bucket
false bottom
soda lime

Yellow Springs Instruments telethermometer and temperature probe; 2) acclimation period of at least 30 min to allow the bird to come into thermal and moisture equilibrium within the chamber; 3) measurement of pressure change within the chamber from between 15 to 60 min; 4) continuous monitoring of chamber or ambient temperature; and 5) body weight. Expired carbon dioxide (CO2) was absorbed by placing soda lime inside the chamber. The change in pressure between the chamber and outside air was determined by reading the change in height (h) of the water column (mm) on a manometer. To convert h into O2 consumed ($\dot{V}O2$) per g of bird per hr, the following equations were used: $K = [(V - W) \times 273/T] / 10{,}340$ (ml H_2O) (Umbreit, 1972); $K \times h = X$ ($\dot{V}O2$/ unit time); $X/W(g) = \dot{V}O2/g/\text{unit time}$; where K is the flask constant, V is the volume of the chamber (ml), W is body weight (g) used as an approximation of the volume of the test animal, and T is the chamber temperature (C). The $\dot{V}O2$ can be converted into calories (cal) by multiplying by 4.8 (Dawson, 1974). Two chicks from Baccalieu Island were tested every other day up to 21 days (n=17), and on Great Bird Rock 16 chicks up to 21 days (n=47) Four breeding adults (during the incubation stage) were also tested.

Studies of growth energetics and dynamics often use captive nestlings due to logistical problems in using wild nestlings (e.g., Kahl, 1962; Schreiber, 1976; Kushlan, 1977; Cooper, 1978). This method allows direct measurement of the

energy requirements of chicks under captive condtions and an indirect measurement of parental feeding energy output. Before extrapolating results from captive to wild chicks, their rates of development must be shown to be similar. This is usually done by comparing increments in body mass of known aged birds. Field studies yield more direct results since the frequency, type and quantity of feeds are obtained (Dunn, 1975c). There is often difficulty in quantifying the caloric value of feeds. Parental feeds by seabirds often vary in frequency, type and size over the nestling period (Pearson, 1968; Lemmetyinen, 1973; Haymes and Blokpoel, 1978; Kirkham and Morris, 1979). Field methods for caloric intake usually involve collecting (e.g., Westerterp, 1973) or estimating (e.g., Dunn, 1975c) nestling feeds. This study incorporated both field and laboratory techniques in determining caloric intake.

Observations of parental feeding and chick begging behaviour were made from a canvas hide (0.9 X 0.9 X 1.3 m) set up about 7 m from nest sites. Thirteen all-day watches (four in 1978 and 1979 on Funk Island; five on Great Bird Rock, 1979) were conducted. Thirty-six nests were observed, and a total of 1,436 nest-observation hr recorded. About 10 nests were observed during each watch. Study nests contained eggs and chicks between one and 50 days old. The following data were recorded during each watch: 1) duration of daily nest attendance by males and females; 2) nest

change-overs, i.e., when one parent replaced its mate at the nest; 3) frequency of parental feeds (a single feed consisted of an entry by the chick into a parent's mouth beyond the gape with a transfer of a food bolus to the chick). Parents were sexed based on behavioural and subtle morphological differences: a) males stand on females and neck-bite during copulation; b) they also bite or make intention movements toward the female's nape upon every arrival at the nest; c) males collect nest-material; d) during the latter half of the nesting season, females show more white on their foreheads (Nelson, 1978b; Montevecchi and Porter, 1980).

Samples of ingested food items were obtained from three age classes - 1) nestlings; 2) immature-plumaged birds (2-5 years); and 3) mature-plumaged birds (>5 years, usually breeding individuals). Samples from class 1 were collected at nest sites. Class 2 samples were obtained by approaching loafing birds, that often regurgitated their crop contents prior to taking flight. Class 3 samples were collected either at nests or from individuals loafing at the periphery of the colonies. Samples were identified to species and weighed with 300 and 500 g Pesola spring scales. Nestlings that regurgitated were weighed to estimate age. Most food samples were collected on Funk Island and Great Bird Rock.

RESULTS

I. Nestling Development

I.1. - Growth

In Newfoundland, hatching begins in the latter part of June and peaks in early July. Newly hatched chicks were found as late as the second week of August. Hatching weights (X $\pm$ SD, n=6) were 83.7 $\pm$ 7.5 g. During the first 3 weeks, chicks gain weight rapidly, obtaining about one third of their eventual adult weight. By 7 weeks, chicks attain adult weight and surpass it by up to 50% by week 9 (Figure 3). Linear regression analysis of the weights of chicks from 0 to 60 days yields a highly significant line fit ($r=0.980$). After 60 days, the weight curve asymptotes, though there is large variation between chicks. Up to 21 days, captive chicks grew at rates similar to those of wild chicks at Great Bird Rock and Baccalieu Island (Figure 4). There was no significant difference in elevation and slope of the regression lines for weight increases of captive chicks ($Y=-327.12 + 73.92\ X$) and Nelson's (1964) wild chicks ($Y=-257.45 + 75.55\ X$) from hatch to 60 days (t-test, $p>.05$; Zar, 1973). Chicks continued to gain weight up to 8 weeks, after which captives were substantially heavier than wild chicks till beyond fledging age (week 14, Figure 3). The growth rate constant (K) for Northern Gannets, calculated using the logistic equation, is 0.063 (Ricklefs, 1968a, 1973). The growth constant, is similar to the growth rates

Figure 3 - Weight gain of captive and wild (adapted from Nelson, 1964) chicks from hatch to fledging (A-adult weight, F-fledging).

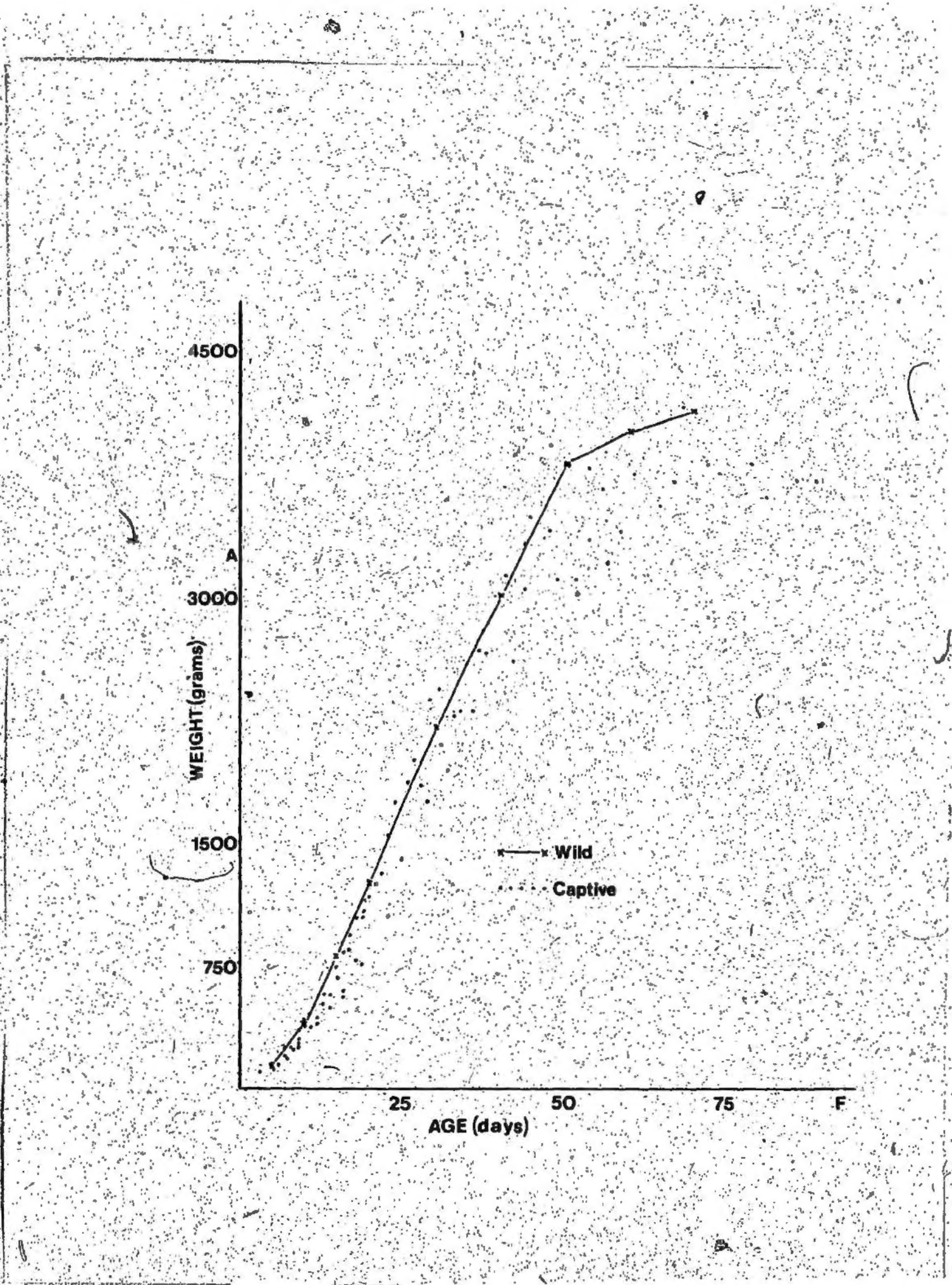
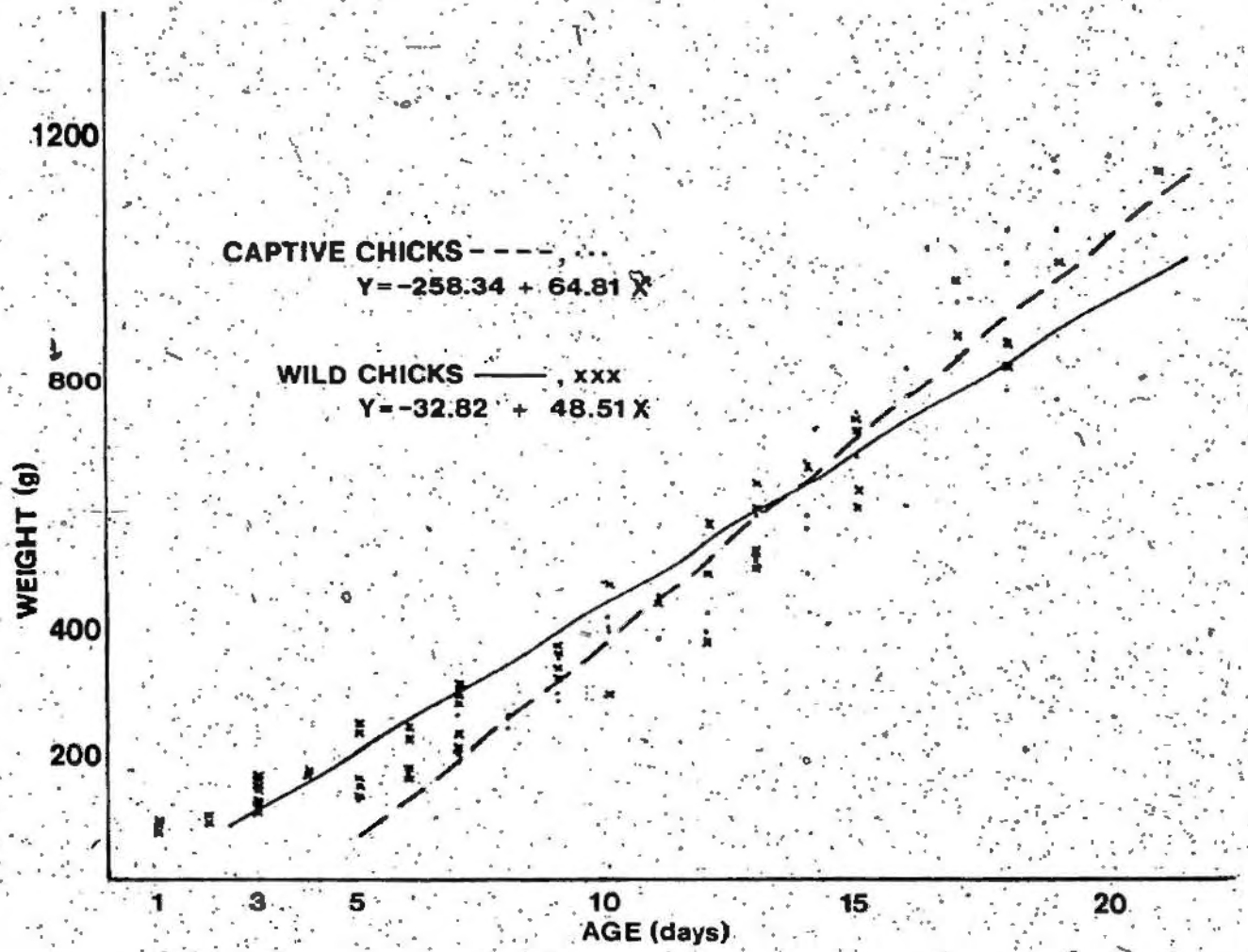

4500
A
3000
WEIGHT (grams)
1500
750
Wild
Captive
25
50
75
F
AGE (days)

Figure 4 - Linear regression of weight on age for captive and wild chicks from hatch to 21 days.


CAPTIVE CHICKS - - -, ...
Y = -258.34 + 64.81 X
WILD CHICKS ——, xxx
Y = -32.82 + 48.51 X
1200
800
400
200
WEIGHT (g)
1
3
5
10
15
20
AGE (days)

of altricial land-birds that also lay a single egg, and almost as rapid as those seen among altricial species that lay more than one egg (Ricklefs, 1973).

Hatchlings have well developed tarsi and midtoes in relation to proportionate adult size compared to other body parts. By 3 weeks, the tarsi are fully grown, and the feet reach adult length by week 4 (Figure 5). The rapid growth of the tarsus and midtoe is linked directly with nestling activities, e.g., receiving food, temperature regulation, and wing-flapping, and will be discussed later. The chick's bill is small relative to adult length at hatching, though it approaches adult length at about the same rate as the midtoe (Figure 6).

The wing is the slowest growing external part of a nestling. At hatching it is about 10% of adult length. The wing reaches adult length at or slightly after fledging age (Figure 6).

In view of the five regression lines in Figure 6, the wing provides the most reliable measure of age ($Y=-1.98 + 0.54X$, $r=0.994$), followed by (in decreasing order of accounted variance): weight ($Y=-327.12 + 73.92X$, $r=0.980$), culmen ($Y=15.91 + 1.61X$, $r=0.978$), midtoe ($Y=3.10 + 0.18X$, $r=0.902$), and tarsus ($Y=1.58 + 0.16X$, $r=0.886$). All regression lines shown in figures have homogenous variance and have been standardized to percent adult size.

Photographs and estimates of down cover for several

Figure 5 - Linear regression of tarsus and midtoe length on age from hatch to 30 days (A-adult length of midtoe, Al-adult length of tarsus).

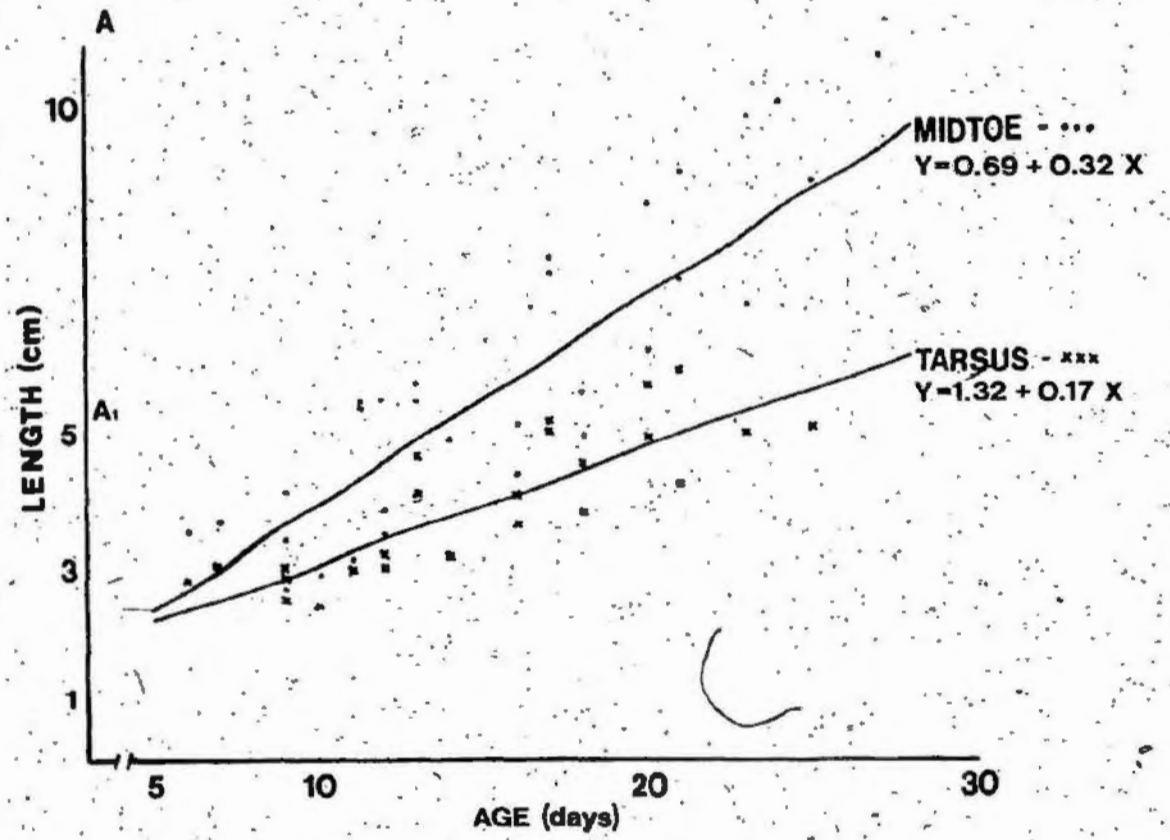
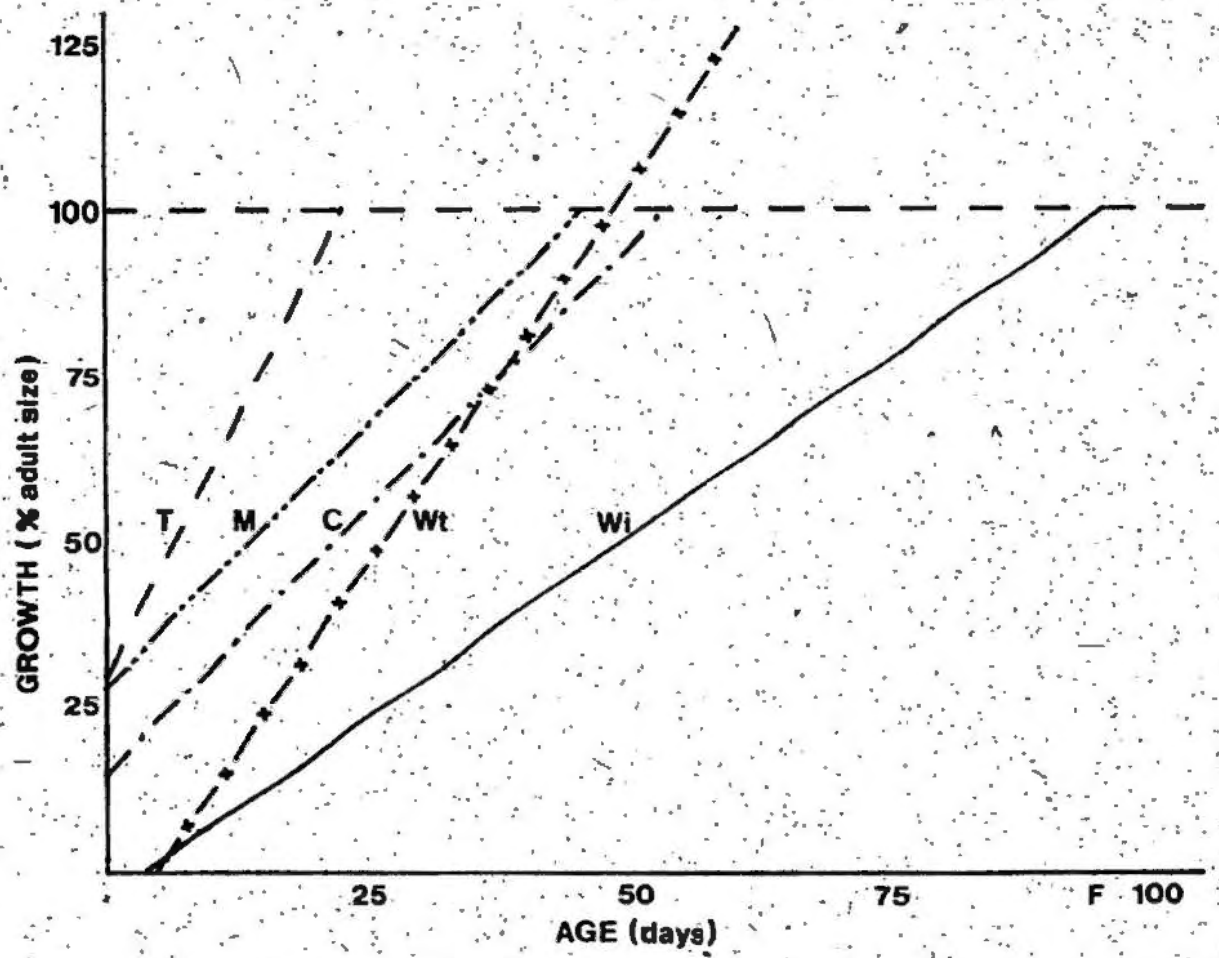

A
10
5
3
1
A1
LENGTH (cm)
MIDTOE - •••
Y=0.69 + 0.32 X
TARSUS - xxx
Y=1.32 + 0.17 X
5
10
20
30
AGE (days)

Figure 6 - Linear regression of all growth measurements (T-tarsus, M-midtoe, Wt-weight, C-culmen, and Wi-wing) on age from hatch to fledging-F.


125
100
75
50
25
GROWTH (% adult size)
T
M
C
Wt
Wi
25
50
75
F 100
AGE (days)

chicks have shown that the back is fully downed by day 11, and the belly by day 17 (Figure 7). At hatching, the belly is completely naked with down first appearing by the end of week 1. Down accumulates evenly on the ventral surface, but is slightly variable between individuals. Accumulation on the back is more crucial than on the belly, because the parents brood young on the top of their highly vascularized webs. When exposed, chicks are vulnerable to the climate from their backside. The dorsal surface has traces of down by day 1 with individuals having slightly more or less. The down does not accumulate evenly and progresses in the following stages: day 1 - virtually naked, sparse scattering of down filoplumes; day 3 - the six wing-tracts are visible but essentially bare, neck and head sparse, back has visible tracts (Figure 8a); day 7 - hip and scapular regions covered but sparse between joints; cloaca, wings, head and neck bare; day 11 - head and neck filling in, back fully covered, wings still quite naked (Figure 8b); day 13 - wings now covered and down is long and fluffy; day 15 - chick is completely covered with down, but may be sparse on forehead and cheek areas.

I.2 - Oxygen Consumption

The rates of oxygen consumption for chicks (n=18) from 1 to 21 days were measured using the apparatus diagramed in Figure 2. Of the power, exponential and linear analyses used, the exponential curve provided the best fit (r=0.634;

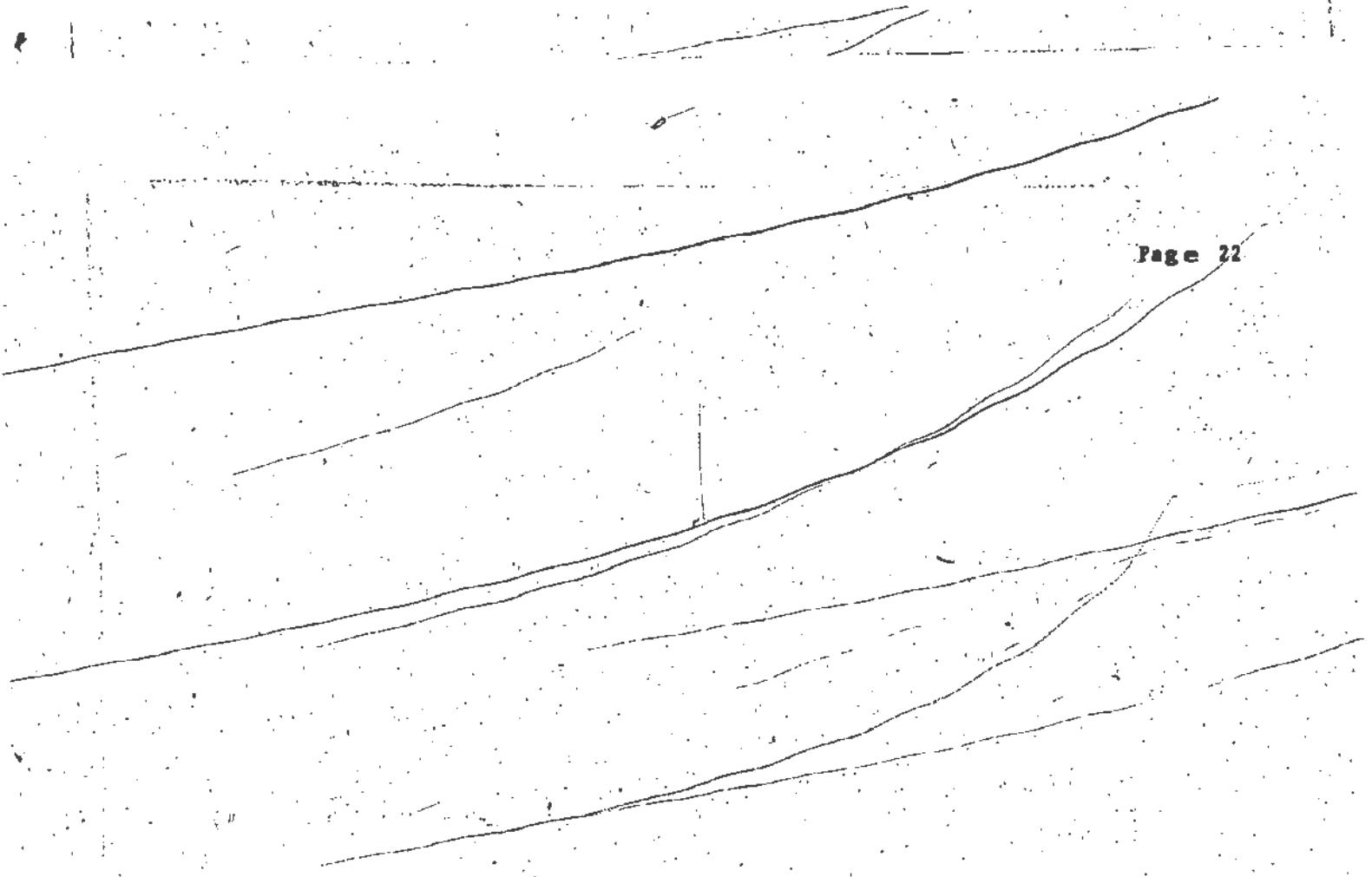


Figure 7 - Percentage of dorsal and ventral down cover during neonatal development.

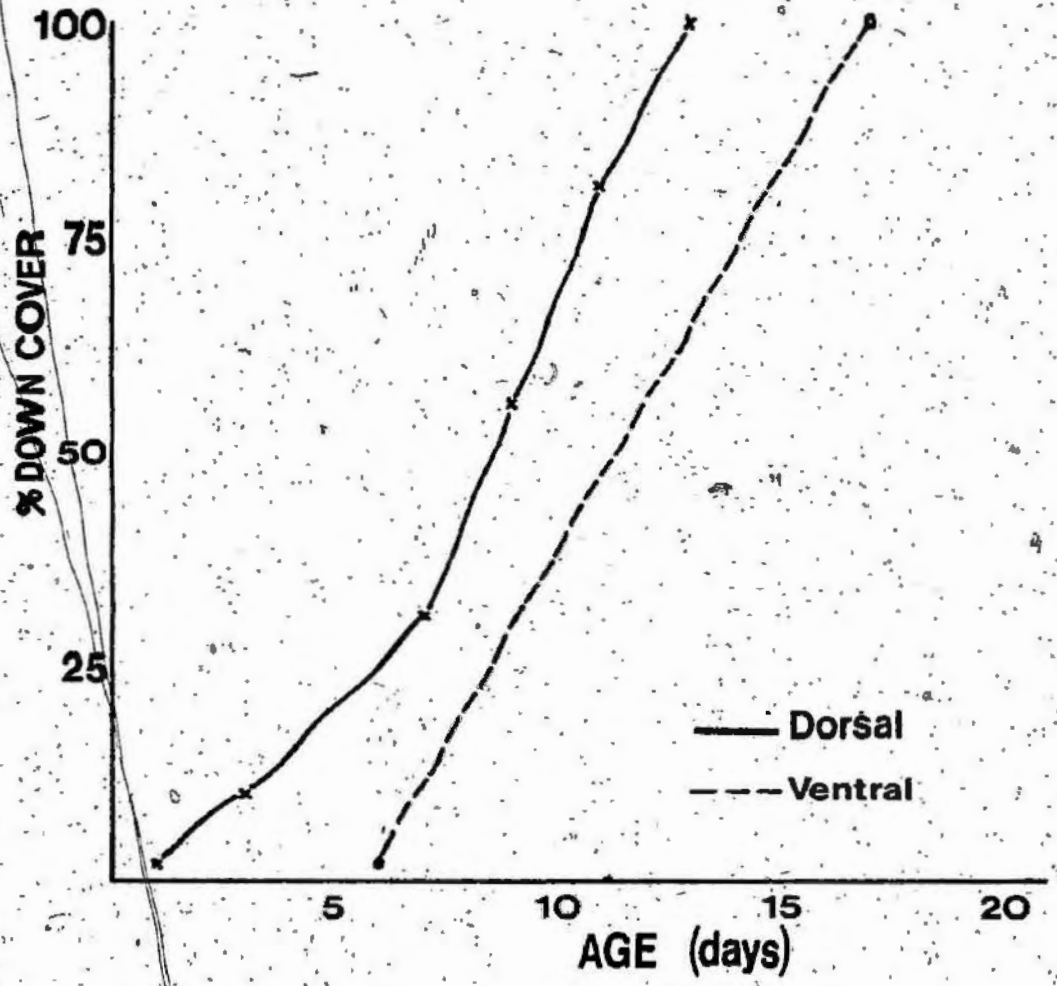

100
75
50
25
% DOWN COVER
5
10
15
20
AGE (days)
Dorsal
Ventral

Figure 8 - Down cover: a) chick 3 days, b) chick 11 days.

Figure 9). Most of the unaccounted variance was due to the curve fit, especially between 5 and 10 days, and the curve should possibly be higher than shown. Oxygen consumption tends to decrease with age, and there was less variability among the measures of older chicks. The four adults tested had a mean (±SD) consumption rate of 0.173 ± 0.063 cc/g/h. The relationship between Ta and body temperature (Tb), when chicks were removed from metabolism chambers, indicates the age at which endothermy is attained (Figure 10). Chicks up to 10 days could not maintain body temperature at low ambient temperatures (Figure 10a). Chicks older than 10 days (Figure 10b) showed greater stability in body temperature, and chicks 16 days and older appeared endothermic.

1.3 - Food and Feeding

Nelson (1978a,b) describes chick feeding rates in terms of the number of feeding bouts. A feeding bout usually consists of several entries by the chick into the parent's mouth, with each entry being up to a few minutes apart. Each time a chick entered the parent's gape it did not always result in a feeding. Older chicks (week 4) beg vigorously and often induce the parent to gape before it is prepared to feed, consequently the chick does not receive any food. Feeds expressed in the results, represent entries which led to a transfer of food from parent to chick.

Gannets feed offspring by partially regurgitating the

Figure 9 - Exponential curve fit of oxygen consumption of wild chicks (n=18) from hatch to 21 days and adults (x, n=4).

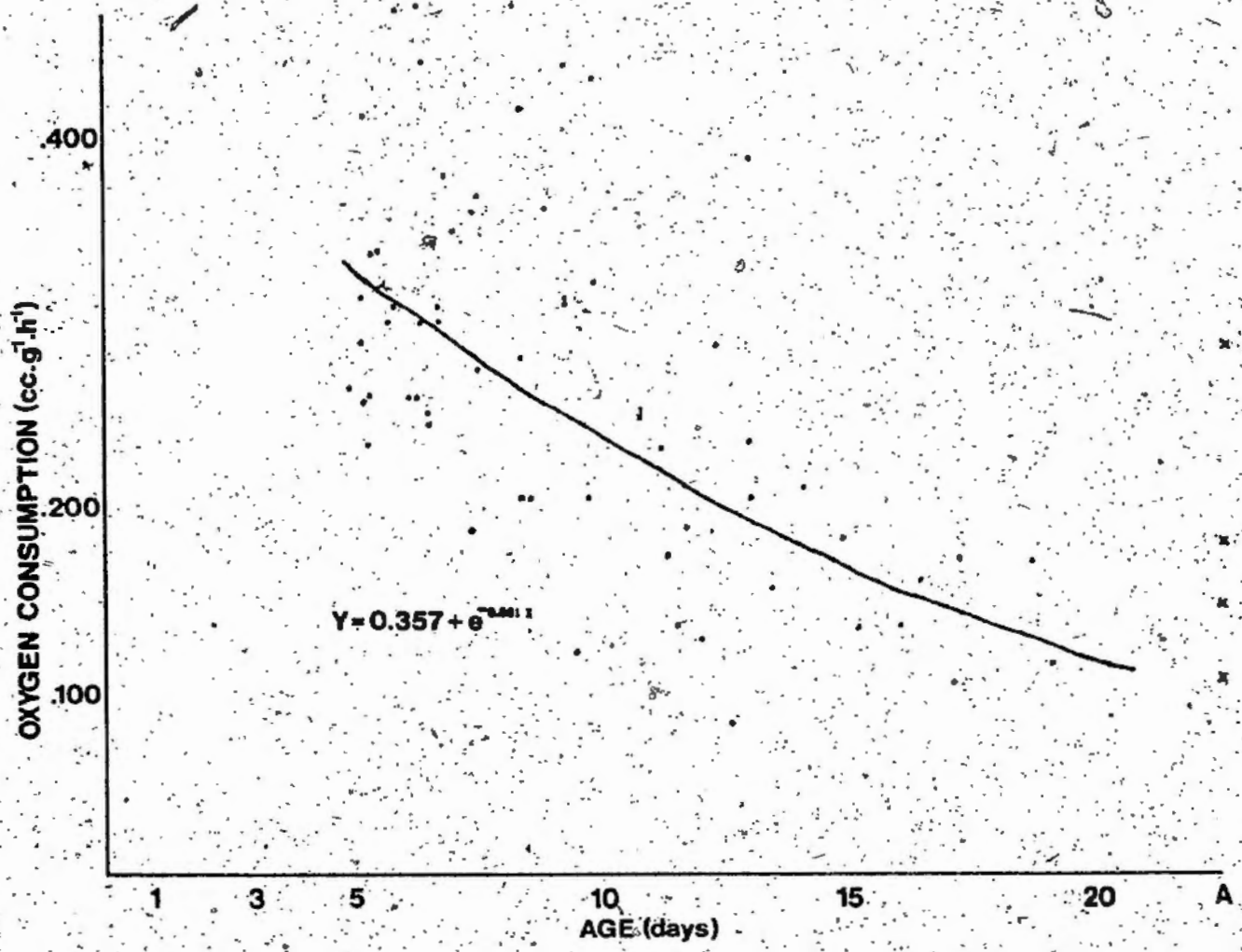
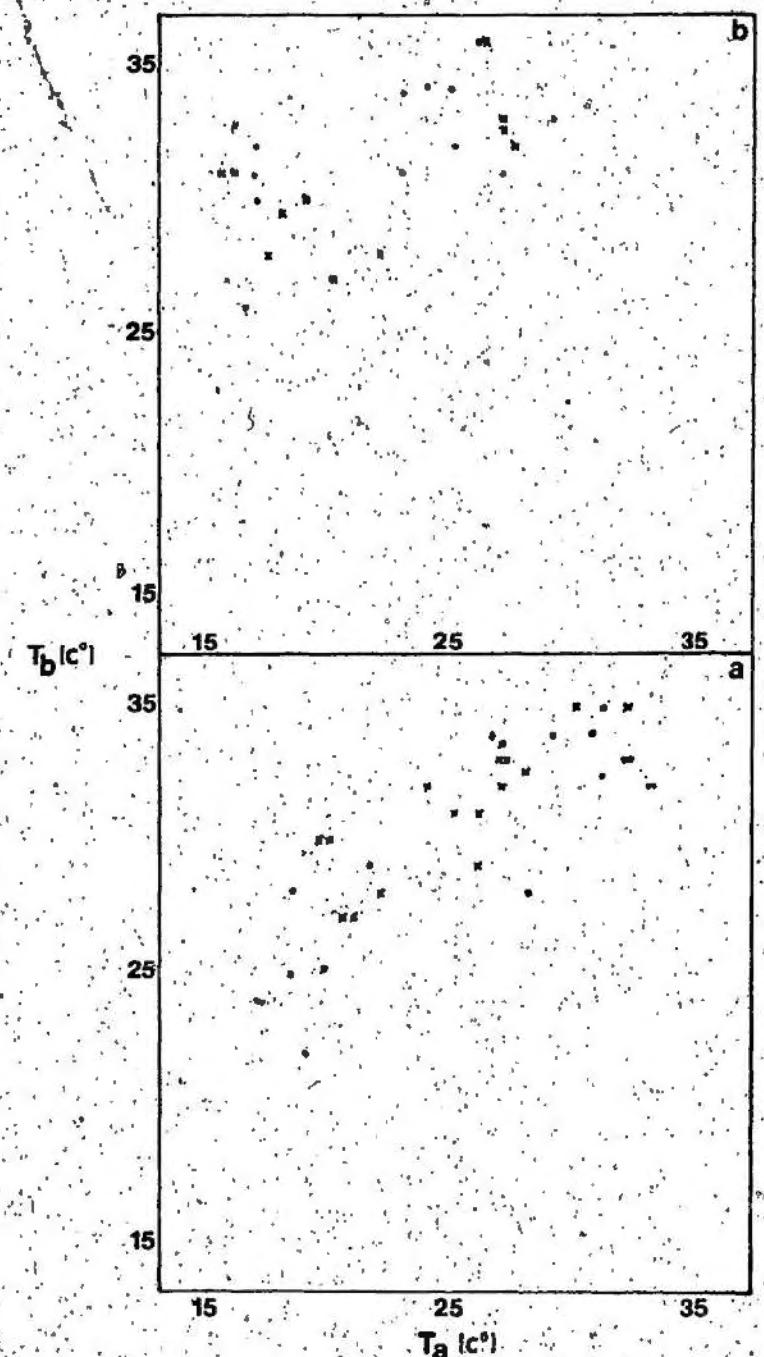

.400
.200
.100
OXYGEN CONSUMPTION (cc.g⁻¹.h⁻¹)
Y = 0.357 + e
1
3
5
10
15
20
A
AGE (days)

Figure 10- Body temperature (Tb) versus ambient temperature (Ta) of various aged chicks.
a) hatch to five days(o), six to 10 days(x).
b) 11 to 15 days(o), 16 to 21 days(x).


b
a
35
25
15
15
25
35
T_b (c°)
T_a (c°)

food bolus to their gape where it is transferred to the chick. The chick, immediately before feeding, stretches its neck and pushes up with its legs (Figure 11a,b). The chick, inserts its head into the parent's mouth and gapes. The bolus then slides into the chick's mouth, which acts like a funnel (Figure 11c). The lower mandible is distensible and can be stretched outward as far as the gular pouch will allow (approximately 12 cm at the hinges).

Daily feeding rates of chicks are initially high, peaking in week 3, declining thereafter (Table I). Chi-square analysis was used to test for sex differences in parental feeding. Although the samples are not completely independent, this analysis is more conservative and applicable than a Cochran Q or McNemar test. Three Chi-square tests were performed on: weeks a) 1, 2 and 3, b) 4-7, and c) 1-7. The results for tests a) and c) indicate that males delivered significantly ($p<.001$) more feeds than females. Test b) revealed no sex difference in parental feeds ($p>.05$). While males delivered more feeds overall, they differed significantly from females primarily during the first 4 weeks post-hatch. The mean caloric content of feeds increased steadily from hatch to week 7 (Table I).

As mentioned previously, captive and wild chicks grew at similar rates up to week 8. The foods fed to captive chicks were similar to what wild chicks received. Chicks were fed primarily capelin (Mallotus villosus) during the

Figure 11- Feeding sequence (chick approximately 3 weeks)
a) parent stimulates head, chick stretches neck
b) chick pushes up, parent gapes
c) chick gapes, note bolus in parent's throat.

Table I - Feeding rates and caloric value of feeds from hatch to week 7.

Table I - Feeding rates and caloric value of feeds from hatch to week 7.

AGE (WEEKS)	FEEDS MALE	FEEDS FEMALE	TOTAL	$\bar{X}$ FEEDS /NEST /DAY	MEAN KCAL /$\bar{X}$ FEED[3]	MEAN KCAL /DAY[3]	MEAN KCAL /WEEK[3]
1	22	10	38	5.6	7.6	42.7	299.1
2	55	20	93	6.9	17.1	117.8	824.5
3	52	30	88	7.8	29.9	233.1	1631.5
4	12	2	14	3.9	112.5	438.8	3071.5
5	0	0	0	3.6[2]	175.0	621.3	4349.2
6	0	7	7	3.2	270.9	866.8	6067.7
7	3	1	4	1.8	367.5	661.5	4630.3
4-7[1]	45	49	94	3.3	193.2	647.1	4529.7
1-7	174	109	313	5.3	80.4	426.0	2982.0

[1] Includes 5 additional nests from Funk I., 1978.

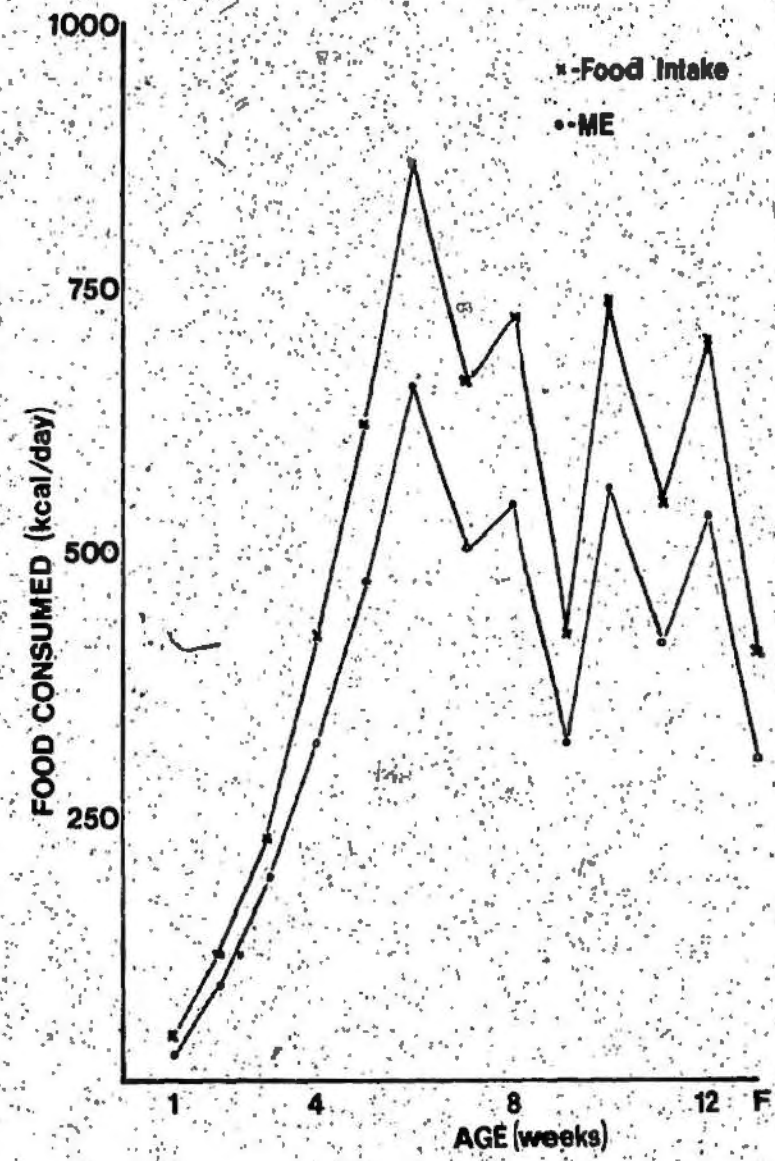
[2] Average $\bar{X}$ feeds/nest/day, from weeks 4 and 6.

[3] Based on the caloric value of foods fed to captive chicks (see Results and Figure 12).

first 4 to 5 weeks and afterwards mostly mackerel (Scomber scombrus). Squid (Ilex illecebrosus) were also fed periodically. The nutritive value of the foods expressed in terms of their metabolizable energy (kcal/g, wet weight) are: mackerel 2.45, sand launce (Ammodytes hexapterus) 1.53, capelin 1.08, squid 0.97. Mackerel is a fatty fish with a 18.6% fat content, as compared to launce (7.8%), capelin (6.0%), and squid (3.0%); for percent composition of water, protein, lipid and ash of these foods, see Montevecchi and Porter (1980). The caloric values of foods consumed by captive chicks are expressed as daily averages at different ages (Figure 12). The mean total food intake from hatch to fledge was 45,545 kcal.

To calculate daily metabolizable energy (ME) of captive chicks, the feces must be weighed, analyzed for caloric value and subtracted from food intake. Unfortunately this was not done, though two feces samples were collected from two captive chicks about 6 weeks of age. The energy excreted in these samples were 3.316 and 3.037 kcal/g (10.34 and 13.77 g dry weight, respectively; mean = 3.117 kcal/g). Cooper (1978) analyzed the energy excreted from captive South African Cape Gannets (Morus capensis) and obtained a mean value of 3.07 kcal/g. Cooper found no significant change in the energy content of excreta over the nestling period, and calculated a mean assimilation efficiency ([kcal intake - kcal excreta] / kcal intake) of 76.1%. Since the

Figure 12- Record of food (kcal) fed to captive chicks (n=2) and estimated metabolizable energy (ME) from hatch to fledging-F. Week 1(1978), weeks 2-13(1979).


1000
750
500
250
FOOD CONSUMED (kcal/day)
×-Food Intake
•-ME
1
4
8
12
F
AGE (weeks)

relative increase in body mass and the energy content of feces, of Cape and Northern Gannets are similar, it will be assumed that assimilation efficiencies are also similar, as are those of other fish eating marine birds (e.g., Dunn, 1975a). The mean daily values for ME based on this assumption are plotted in Figure 11. The mean total ME is estimated to be 34,660 kcal.

The substantial weight increase during the first 5 weeks was due to increasing food consumption, which was more or less stable from week 6 (wild chicks typically reach a peak weight during weeks 8-10). Another factor contributing to the rapid increase in daily caloric uptake is the change in diet from capelin to mackerel, and its higher fat content. From weeks 7 to 13, chicks consumed on average 598 $\pm$ 130 kcal/day. This value is slightly inflated during the last three weeks since wild chicks receive on average fewer feeds per day as they approach fledging age. A more realistic value for week 13 is 299 $\pm$ 224 kcal/day, based on the mean number of observed feeds (0.4; from Montevecchi and Porter, 1980) and the mean ($\pm$SD) weight of mackerel regurgitations from adults (305 $\pm$ 100 g, n=81; see Discussion).

Regurgitations from both adults (n=805) and sub-adults (non-breeders, n=86) were identified and in many cases weighed. The frequency of food types collected both years from the three gannetries are given for adults (Table II)

Table II- Frequency (percentage of total) and the mean (±SD) weights (g) of regurgitated food types by adults across season and colonies.

Table II - Frequency (percentage of total) and the mean (±SD) weights (g) of regurgitated food types by adults across season and colonies.

Food Type	Great Bird Rock, 23/5-4/7/79	Funk I., 9/7/78	Baccalieu I., 1-31/7/78	Funk I., 31/7-6/8/79	Funk I., 11-20/8/78	Total(%)
Scomber scombrus #	79 (33)	68 (21)	15 (68)	103 (57)	18 (47)	283 (35)
X̄±SD wt(n)	275±119(7)	—	217±25(15)	303±103(41)	432±136(18)	
Scomberexos saurus #	—	—	1 (5)	26 (15)	16 (42)	43 (5)
X̄±SD wt(n)	—	—	250 (1)	214±103(12)	301±112(13)	
Ilex illecebrosus #	1 (0)	38 (11)	1 (4)	33 (18)	4 (11)	77 (10)
X̄±SD wt(n)	—	—	200 (1)	145±64(15)	45 (1)	
Clupea harengus #	—	2 (1)	—	16 (9)	—	18 (2)
X̄±SD wt(n)	—	—	—	341±87(5)	—	
Ammodytes hexapterus #	154 (65)	—	—	—	—	154 (19)
X̄±SD wt(n)	158±55(44)	—	—	—	—	
Miscellaneous #	2 (1)[1]	216 (65)[2]	5 (23)[2]	1 (1)[3]	—	2 (0)[1]
X̄±SD wt(n)	164 (1)	6 (2)[3]	91±18(5)	130 (1)	—	221 (27)[2] 7 (1)[3]
Total	236 (100.1)	330 (100)	22 (99.9)	179 (99.9)	38 (100)	805 (100)
Mean ± regurgitation weight in g(n)	174±77(52)		189±55(22)	257±115(74)	360±148(36)	(184)

[1] Ocean perch (Sebastes marinus)
[2] Capelin
[3] Tomcod (Microgadus tomcod)

and sub-adults (Table III). Mackerel was the most frequent food type during July (Baccalieu Island) and August (Funk Island). In August 1978, Atlantic saury (Scomberexos saurus) was nearly as frequent as mackerel, but not in 1979. Capelin was also common in early July. Inter-colony differences in food type were mainly between Great Bird Rock and the Newfoundland colonies. Sand launce was the most common food at Great Bird Rock, while none were collected at Newfoundland gannetries. Saury were not found at Great Bird Rock, and squid and mackerel were obtained at all colonies. (Some of the differences between colonies is likely due to temporal differences in sampling and is possibly a reflection of seasonal abundances.) Mean adult regurgitation weights (food types pooled) across the season were as follows: 149g in May, 114g in June, 217g in July, and 360g in August. Regurgitations collected from both immature-plumaged (non-breeding, Table III) birds and adults (Table II) on Funk Island differed significantly (t-test, $p<.01$) in weight during mid-August (1978), but did not in early August (1979). Adults regurgitated roughly 40% more fish than non-breeding birds during mid-August, which may also reflect the food demands of older nestlings.

II. ADULTS

II.1. - Incubation and Brooding

The incubation period is roughly 6 weeks long during which time both the male and female share in caring for the

Table III-Frequency (percentage of total) and the mean (±SD) weights (g) of regurgitated food types by immature-plumaged birds across season and colonies.

Table III - Frequency (percentage of total) and the mean (±SD) weights (g) of regurgitated food types by immature-plumaged birds across season and colonies.

Food Type		Funk I., 31/7-6/8/79	Funk I., 11-20/8/78	Total (%)
Scomber scombrus	#	25 (83)	28 (50)	53 (62)
	X̄±SD wt(n)	292±95 (25)	280±97 (19)	
Scomberexos saurus		1 (3)	24 (43)	25 (29)
		170 (1)	161±65 (19)	
Ilex illecebrosus		3 (10)	4 (7)	7 (8)
		175±57 (3)	65 (1)	
Miscellaneous		1 (3)[1]	—	1 (1)[1]
		120 (1)	—	
Total		30 (99.9)	56 (100)	86 (100)
Mean ± regurgitation weight in g(n)		270±101 (30)	229±107 (44)	

[1] Salmon (*Salmo salar*)

egg. Incubation shifts for females averaged 78% (359.5 hr) of the daily nest attendance during all-day watches, while males averaged 22% (99.2 hr; Table IV). Chicks are brooded continuously for the first two weeks and occasionally up to three weeks. Throughout weeks 1 to 7, males attended the nest for 46% (446.2 hr) of the day and females attended for 54% (531.2 hr). Multiple regression analysis of nest attendence by males and females for three different stages in the nest cycle (INC, PH1-3, PH4-7) indicate that time in attendance at the nest (sexes pooled) did not change significantly ($F=0.63$, $p>.05$). The statistical interaction between season by sex was significant ($F=11.51$, $p<.001$). Primarily due to longer incubtion spells, females spent significantly more time on the nest ($F=28.65$, $p<.001$). Males make more trips to the nest-site than females, often bringing nest-material to the female. Gannets engage in nest-building throughout the incubation and nestling periods, with almost all of the material being collected by the male.

Table IV- Average (±SD) incubation and brooding shifts to week 7, by males and females (INC-incubation, PH1-post-hatch week 1).

Table IV - Average (±SD) incubation and brooding shifts (min) by males and females (INC-incubation, PH1-post-hatch week 1).

Nest Stage	Time at Nest					No. Nests
	Male	(%)	Female	(%)	Total	
INC	192.8±268.7	23.3	633.4±249.4	76.7	27,522	32
PH1	485.3±329.9	51.9	449.7±329.5	48.1	3,740	4
PH2	496.0±288.3	54.1	421.6±294.8	45.9	14,681	16
PH3	335.5±307.0	37.7	553.4±319.6	62.3	9,775	11
PH4	250.0± 10.0	32.1	527.5± 22.5	67.9	1,555	2
PH5	394.2±157.4	44.0	502.5±129.6	56.0	5,380	6
PH6	562.5±182.5	72.3	215.0±170.0	27.7	1,555	2
PH7	299.7±158.2	37.9	492.0±171.7	62.1	2,375	3
PH4-PH7[1]	357.0±190.7	43.4	466.0±188.0	56.6	30,450	37
PH1-PH7[1]	393.7±247.8	45.7	468.7±245.5	54.3	58,646	68
INC-PH7[1]	324.4±271.4	38.1	526.1±255.0	61.9	86,168	100

[1] Includes 24 additional nests from Funk Island, 1978, that contained chicks of ages between 4 and 7 weeks post-hatch.

DISCUSSION

Growth, Temperature Regulation and Metabolism

The growth of nestling gannets involves various changes in morphology, physiology and behaviour. Many of the physiological changes, such as the development of homeothermy, are causally associated with morphological and behavioural changes.

According to Ricklefs (1979b) the growth rate of an organism is best determined by the slowest growing body component. In Northern Gannets, the wing is the slowest growing component and does not fully mature until after fledging. Cape Gannets also show linear increases in wing length reaching adult size after fledging (Cooper, 1978). In comparison, the slowest growing body part of precocials is often the tarsus. The acquisition of functional maturity of body parts is related to the time when growth approaches its asymptote (Ricklefs, 1979b). The loss of water in tissues is also a measure of functional maturity (e.g., weight recession and plumage development). The gannet's tarsi mature first, followed successively by the midtoes, culmen and wings (body weight is considered separately).

The rapid growth of the tarsi and midtoes is linked directly with nestling temperature regulation and feeding. The tarsi (reticulate) and feet (totipalmate) are structured such that movement on land is slow and awkward, since the gannet's center of gravity is in front of the hip joints.

The method of chick feeding requires the nestling to push upward with its feet and to stretch its neck up into the parent's gular pouch (see Figure 10c). Thus for efficient reception of food, nestlings need well developed neck and leg muscles and proper body support (midtoe).

Ricklefs, Montevecchi, Kirkham, and Gabaldon (ms) analyzed the composition of various body parts and organs in different aged gannet nestlings. The lipid-free (wet) weight of the head, brain and leg muscles of gannet chicks all increased to near adult levels by week 4. Similar trends have been reported for other altricial nestlings (O'Connor, 1977). The relatively large size of the brain and head is associated with a large gape and culmen, and consequently a greater capacity for increased food size.

The second important function of rapid tarsus, midtoe and culmen growth is in temperature regulation. All three body parts are of primary aid in heat loss. Culmen size corresponds with the size of the gular pouch. Gular fluttering facilitates heat loss through evaporation (Bartholomew, et al., 1968). The pouch is highly vascularized as are the webbed feet. When heat-stressed, nestlings typically extend their legs and webs out from under their body. The wings are drooped outwards and the nestling, by all visual appearances, looks dead. Chicks often defecate directly into the nest which provides a cool substrate. When placed on a hot substrate, chicks raise

their body and begin to gular flutter (Harvey, 1979). Cape Gannets respond to high ambient temperature initially by standing, followed by gular fluttering and wing drooping (Cooper and Siegfried, 1976). The ontogeny of gular fluttering has not been investigated, but appears very well developed at hatching (Montevecchi, unpubl. data).

The transition from poikilothermy to endothermy also involves the ability to produce and retain body heat. Shivering and muscular activity appear to be the primary sources of heat production, since non-shivering thermogenesis has not been observed in birds (Steen and Enger, 1957; West, 1965). Leg shivering is not fully developed in gannets until week 3 (Montevecchi, pers. comm.). Growth pectorals is slow relative to other muscles (Ricklefs *et al.*, ms) and is probably not important in the development of nestling temperature regulation.

Increase in body mass corresponds to a decreasing surface to volume ratio (Calder, 1974). There is a general decreasing trend of thermal conductance with increasing body size. The increase in body weight would therefore enhance heat retention, however a complete covering of down filoplumes is essential for maintaining body temperature. It was found in the present study that nestlings have a complete covering of down on the back by day 11, and are fully downed by 17 days. Gurney (1913) states that gannets are fully downed by 11 days, while Nelson (1978a) says that

down accumulation is complete by week 3. The slower development of ventral down compared to dorsal growth corresponds to the adult's method of brooding chicks on top of their webbed feet.

Since the feet and gular pouch are used as sources for heat loss, they must be covered when the chick is cold-stressed. When subject to cold ambient temperatures, Cape Gannets sit on their webs and cover their bill beneath the wings (Cooper, 1979). Northern Ganneta are brooded continuously during the first two weeks, and occasionally during the third week. Hatchlings cool quickly on removal from the nest. Body temperature, relative to ambient temperature, is maintained by around 16 days, indicating the achievement of effective endothermy (also the age when adult brooding ends). At this stage in nestling growth, the tarsi, midtoes, culmen, down cover, capacity for gular fluttering and shivering are all well developed.

The age of endothermy in northern seabirds other than gannets varies considerably, according to developmental mode, growth rate and body size. The attainment of endothermy ranges from the day of hatching (e.g., Eider Ducks, Somateria mollissima) to 2 weeks post-hatch (e.g., Double-crested Cormorants, Phalacrocorax auritus; Dunn, 1975b, 1976a,b, 1979). Masked Booby (Sula dactylatra) nestlings, the only other sulid in which homeothermy has been studied, are endothermic at 18 days (Bartholomew,

1966). Effective endothermy in gannets is marked by the development and maturity of various body components (e.g., full down cover) and also represents the first stage in chick independence (e.g., cessation of parental brooding).

As in many other oceanic birds, gannet chicks show a weight recession prior to fledging. Ricklefs (1968b) found weight recession to be confined to seabirds, swallows and swifts, species that spend long periods of time on the wing. The drop in nestling weight appears correlated with a loss of water as integument tissues mature (Ricklefs, 1968b). O'Connor (1975) has also found weight recessions in House Martins (Delichon urbica), House Sparrows (Passer domesticus) and Blue Tits (Parus caeruleus), though it is particularly small in the latter two species. A gannet chick may exceed adult weight by up to 50% due primarily to a large deposition of fat stores (Nelson, 1978b; Ricklefs et al., ms). The subsequent weight recession after week 9 is also due to an increase in nestling activity (e.g., wing-flapping), a decline in parental feeds (Montevecchi and Porter, 1980), and possibly a decreased motivation to feed by chicks (e.g., Cooper, 1978).

At fledging, Northern Gannet nestlings do not actually take flight, rather they jump and, if successful, glide down from the nest riding updraughts and wind currents to the sea. At this time, the parent-young bond is severed. It is thought that the chicks remain on the water for a couple of

weeks during which time they acquire fishing skills while subsisting on their fat reserves (Nelson, 1978a). The gannets' plunge-diving method of fishing is specialized and it is likely that immature birds take some time developing these foraging skills.

The metabolic rate of wild nestlings declined to adult levels and became less variable when they reached the age of endothermy. Endothermic chicks and adults differed in their oxygen consumption from the Aschoff and Pohl (1970) equation for resting non-passerines by being 23% (n=9) and 37% (n=4), respectively, of the predicted adult value. Poikilothermic chicks (5 days, n=5) consumed oxygen at a rate of 41% of that predicted for adults of similar weight. Dawson et al. (1976) compared measured basal metabolic rates (BMR) with values from various predictive equations. They found a high degree of variability between orders of birds ranging between 65-90% for ducklings and 40-72% of predicted values for gallinaceous birds. The Aschoff and Pohl (1970) predictive equations for passerines and non-passerines are based on 14 and 17 studies respectively. The largest altricial species in these studies was the Hooded Crow (Corvus corone) which is about one sixth the weight of the Northern Gannet. Metabolic relationships with body size are poorly understood, except in terms of a proportionate reduction in the metabolic power required per gram of body mass (see Calder, 1974).

The low measures of $\dot{V}O_2$ for gannets relative to predicted values may have been a function of the chambers. The chambers used were designed for portability and did not have any mechanism for circulating air, thus the CO_2 produced may not have been completely absorbed by the soda lime. This could have resulted in lower $\dot{V}O_2$ levels. Since all methods were pre-standardized (e.g., quantities of soda lime, and time in chamber) under controlled conditions, it is possibile that the results observed are representative of the metabolic levels of nestlings and adults.

The trend in metabolic change against age in gannets can be interpreted as real, despite the aforementioned points. The decreasing $\dot{V}O_2$ as a function of age (and development of endothermy) of gannets fits with Ricklefs' (1974) schematic representation of BMR and nestling age. This function, in addition to the substantial reduction in $\dot{V}O_2$ measures at week 3, indicates a stabilization in metabolic rate. When chicks are able to temperature regulate, more energy is used in these processes which would result in levels of metabolism which are closer to those of adults. Aulie (1976) speculated that $\dot{V}O_2$ might stabilize when pectoral muscles were fully developed. These muscles are important for thermoregulation in ptarmigan (Lagopus lagopus; Aulie, 1976) but leg muscles are more functional in this respect in gannets. The development of tarsi and associated muscles (Ricklefs et al., ms) are well developed

by week 3, and in accordance with Aulie's speculation that the reduction and stabilization of metabolic rate corresponds with the maturity of leg and associated musculature. Vleck et al. (1977) report differences in $\dot{V}O_2$ between precocial and altricial embryos. Altricials show an exponential increase in $\dot{V}O_2$, whereas precocials have a plateau in $\dot{V}O_2$ before hatching. The authors suggest that the stabilization in $\dot{V}O_2$ of precocial embryos is due to a decline in growth rate, a pattern which occurs in altricials after hatching.

Food and Parental Feeding

The relative size of feeds taken by chicks increased with their ability to receive larger feeds (e.g., culmen growth). The caloric value of individual feeds increased up to week 7 and probably declines shortly afterwards. Feeding rates declined after week 3, the feed sizes increased up to week 7 and then remained fairly stable. The reduction in feeding rates after week 7 is partially responsible for the subsequent weight recession of nestlings. To estimate the amount of food energy fed to chicks from hatching to fledging, the period from weeks 8 to 13 inclusive must be reconciled in terms of weight loss and the decline in feeding rates. It will be assumed that the feeding rate during this period is about 0.7 times daily and that chicks receive mackerel feeds similar in size to the average regurgitation weight (305 $\pm$ 100g). The estimated total for

food intake over 13 weeks thus becomes 42,843 kcal, which is approximately 2,700 kcal below the consumption by captive chicks. The mean assimilation efficiency of Northern Gannets may therefore be higher than the 74.2% value for Cape Gannets, and possibly account for the differences in caloric intake by the two species.

Montevecchi and Porter (1980) found the ratio of begs to feeds, in Northern Gannets, to be about stable (approximately 10:1) up to week 8, at which time the ratio increased dramatically to over 50:1 during week 13. There was an inverse relationship between begging and feeding rates during the last 7 weeks. It is difficult to compare Nelson's (1964) results with Montevecchi and Porter's (1980) since the former recorded the number of feeding "bouts" which consisted of numerous gape entries. In this study, chicks between 1 and 7 weeks post-hatch, 84% (n=660) of the gape entries (n=784) resulted in feeds. Montevecchi and Porter (1980) recorded actual transfers of food to chicks, and their results are very similar to those presented here (Table I). Their data include feeding rates of two additional chick ages (weeks 8 and 13) which fit with the decreasing number of feeds observed here from weeks 3 through to 7. The high number of feeds reported by Nelson (1964) at week 7, most probably reflects increased begging activity and forced gape entries (usually unsuccessful) by chicks.

There was a sexual difference in the frequency of parental feeds during the first 3 weeks post-hatch. Males fed chicks more often during this period, but both sexes fed chicks as frequently afterwards. The small caloric requirement of nestlings up to week 4 probably does not significantly increase the foraging demands of the male much beyond its own maintenance level. Many adult regurgitations of mackerel lacked heads, which had already been digested. Young chicks are frequently fed small amounts of fish, and the adult must reswallow after a feed. Adults therefore digest (and assimilate) portions of the fish delivered to chicks. After week 3, the daily intake by nestlings increases sharply from an equivalent of about 1/2 a mackerel (week 4) to about 1 mackerel (week 6). During this period males and females share more equally the duties of chick feeding.

Parental Investment

Gannets feed on several species of fish, all of which are surface shoaling and of commercial value. Mackerel has a very high caloric value (2.45 kcal/g) relative to other species and is the principle food of North American gannets. The other species commonly caught have an average caloric value of 1.2 kcal/g, which is about the same as the mixture of fish eaten by Double-crested Cormorants (Dunn, 1979). Mackerel are the largest fish caught by gannets, and adults usually regurgitated single whole mackerel. Chicks 6 weeks

and older can handle feeds of entire mackerel, which supplies sufficient food energy for at least one day. Nelson (1978a) cites a long list of fish known to have been caught by gannets. Regardless of colony location mackerel seems to be the most commonly caught species. Fish eaten by Northern, Cape and Australasian Gannets (Morus serrator) are somewhat similar. All species feed on mackerel, various species of needle fish (Scomberesox spp.) and cephalopods (see Rand, 1959 - cited in Nelson, 1978b; Wodzicki and Moreland, 1966; Brun, 1974; Nelson, 1978a,b; this study). The similarity in fish species caught by gannets in three different oceans is related to the common schooling behaviour of these fish and the plunge-diving method of fishing employed by all gannets.

Since single mackerel were the commonest food regurgitated by adults, the average weight of a mackerel regurgitation (305 g) will be used as the daily adult food requirement (about 11% adult weight, which is about 3-5% greater than the requirements of captive fledglings). Thus a daily food intake of 800 kcal becomes roughly equivalent to the caloric value of an average regurgitated mackerel (750 kcal). The additional 50 kcal represents an estimated correction for adults with chicks, as foraging time is slightly longer.

The food requirements of nestlings increase from hatch to week 8 and then decline slightly to a level which is, on

average, similar to consumption at week 5 (568 kcal/day; Figure 11). Adults must increase their foraging by proportionate increments to successfully rear a chick. If adults increased their food catch by 50% (1,200 kcal/day), a male and female together could provide sufficient food energy to rear a single nestling. The average adult regurgitation weight doubled shortly after hatching (early July), which supports the above estimate of increased foraging demands. Foraging demands probably reach a peak when chicks are between 1 and 2 months old (mid-August). This is borne out from the fact that, during this period, significantly larger regurgitations were collected from adults compared to non-breeders.

The cost of foraging in gannets is restricted to the time spent flying and the energy costs of flapping and gliding flight. Time spent away from the nest during the nestling period will be considered foraging time. This assumption is oversimplified since adults may still be in the vicinity of the colony or loafing on the water. The time spent resting on the water during daylight hours is, however, likely to be minimal (Nelson, 1978a). Herein, the term foraging will refer to flight-time.

Gannets feed in inshore and pelagic areas. They are capable of flying at speeds of 65-80 km/hr and travelling up to 500 km in a day (Nelson, 1978a). Gliding versus flapping flight is an obvious method of energy conservation. While

many estimates for flight metabolism are around 13 x BMR (Tucker, 1973), gliding flight in Herring gulls is about 2 x BMR (3.4 x BMR; Baudinette and Schmidt-Nielsen, 1974). Gannets were observed when approaching, departing and when away from colony sites, to intermix gliding with flapping flight.

There have been no direct measures taken of flight metabolism in gannets, but based on wing structure and a relevant study by Hails (1979), an indirect estimate can be made. Hails (1979), compared flight energetics in the hirundines (martins and swallows) and swifts, which are very similar to gannets in several repects. All species have the following similar characteristics: a) a period of nestling weight recession (Ricklefs, 1968b), b) spend long periods of time on the wing and in open spaces, and c) high aspect ratios, or long and narrow wings (gannets have the highest aspect ratio of all British birds; Barlee, 1956). A high aspect ratio reduces the induced and profile power requirements. The hirundines differ significantly from most birds in having much lower (than predicted) metabolic levels during flight. The metabolic limits were found to be between 4.5-5 x standard metabolic rate, or between 50 and 73% lower than predicted values (Hails, 1979). Based on the several parallel behavioural and morphological similarities between gannets and hirundines, a value of 5 x SMR will be adopted as a caloric estimate of gannet flight.

It is difficult to measure foraging efficiency in gannets, firstly because they often forage at great distances from colony sites, and secondly because they rarely bring a fish to the surface in their bill. However, Nelson (1978a) speculates that following a successful dive (from heights up to 15 m) gannets "shuffle-bathe", dipping and shaking their bills, which provides a potential measure of success. Efficiency of prey-capture can be assumed as fairly high, since they usually feed in dense schools of fish.

Plunge-diving is a spectacular and socially attractive behaviour; the pure-white plumage (unlike most seabirds) of a diving or flying gannet can be seen at great distances (fishermen have often used gannet plunge-diving as an indicator of fish location; see Nelson, 1978a,b). It is common to see what begins as one or two gannets diving, quickly turn into a dense flock of plunge-diving gannets. The conspicuous signalling of the white plumage during a plunge-dive enables solitary or flocks of gannets to locate prey quickly and efficiently.

Nest-site attendance by adults reveals the relative time investment by both sexes required to rear offspring. Males invest by establishing and defending nesting territory and by gathering virtually all the nesting material (Nelson, 1978a). Females initially invest energy through egg production. Because production of a single gannet egg (141

kcal) is less calorically valuable than a mackerel (approximately 750 kcal), it is unlikely that females expend more energy than males early in the breeding season (Ricklefs and Montevecchi, 1979; Montevecchi and Porter, 1980).

Females incubate for significantly longer periods than males. The heat for incubation comes in part from the adult's webbed feet and from embryonic metabolism. The embryo contributes progressively more heat as it develops (Drent, 1972). King (1973) first posed the question of whether or not an incubating bird expends additional heat to brood a clutch. Recently, Mertens (1977) and Walsberg and King (1978) showed that the resting metabolism of several passerine species was higher than that of incubating birds. The thermal environment of the nest probably contributes to lowering the cost of incubation. Heat production by the embryo also lowers the incubation energy requirements for adults. The gannet's nest probably does not aid in controlling heat lost during incubation nor does the altricial embryo provide much of the heat for incubation. However it will be assumed that energetic requirements for incubation does not exceed a resting metabolic level (RMR). Converting to basal levels, incubation is roughly 1.7 x BMR (see King, 1974). Differential incubation shifts by sex trade off with effective foraging time, but since females do not collect nest material this factor may be insignificant.

During the first 3 weeks after hatching, males and females brood chicks for about equal periods. Montevecchi and Porter (1980) also found that during PH1 both sexes spend about the same amount of time on the nest. Males, although feeding chicks more often during this time, do not spend significantly longer spells away from the nest. Male attendance thus supports the speculation that they need not increase their foraging catch to satisfy the chick's food requirements. From post-hatching weeks 4 to 7, females are in attendance at the nest for longer periods than males. The corresponding parental feeds during this nestling stage do not indicate any differential sex role. Females may therefore, be taking greater responsibility in the attendance of chicks, and thus reduces their foraging time.

In order that relative reproductive investments by male and female gannets be estimated, time and energy investments must compared. Table V provides a time and energy summary for both sexes from nest-site occupation to chick fledging. It should be remembered that the values appearing in this table are based on numerous assumptions and are rough estimates at best. This summary, for example, does not allow for the energy expended by males to collect nest-material, and defend the nest-site. However, the underlying assumptions apply to both males and females, thus allowing a comparative picture to be drawn. Maintenance values are assumed to be the same for both males and females

Table V - Relative parental investment as a function of time and energy throughout the reproductive period.

Table 7 -- Relative parental investment as a function of time and energy throughout the reproductive period.

Stage	Energy Expended (kcal) Male	Female	Time (days)
Pre-egg			
egg-production[1]	0	141	
adult-maintenance[2]	37,500	37,500	50
Egg			
adult-maintenance[2]	32,250	32,250	43
Chick			
adult-maintenance[3]	72,800	71,400	
feeding[4]	23,533	20,932	91
Total	166,083	162,223	184

[1] from Ricklefs and Montevecchi (1979).

[2] 750 kcal/day x No. days.

[3] PH1-13(♂): 800 kcal/day x 91 days;
PH1-4(♀): 750 kcal/day x 28 days;
PH5-13(♀): 800 kcal/day x 63 days.

[4] based on a chick receiving 3,827 kcal (PH1-4), with 69.5% (♂), 30.5% (♀) feeds, plus 50 kcal for each 750 kcal fed (see Discussion); and 37,016 kcal (PH5-13) to chicks, with 50% (♂), 50% (♀) feeds plus 50 kcal for each 750 kcal fed.

throughout the nestling period. Until the chick hatches, relative parental investments are about equal. Since males collect the nest-material and are territorially more aggressive than females, the male likely invests the same or more than females during the pre-egg and egg periods. During the nestling stage, males initially surpass female investment (PH1-4) by feeding the chick more often. Thereafter, the female participates more in chick feeding, equalling her partner. The total relative investments by both parents appears virtually the same. This similarity in investment is as would be predicted in view of the gannet's long term pair-bond.

From the above estimate, it is possible to make a calculated guess at the total food consumption of gannets in Newfoundland, during a breeding season. There are approximately 18,600 breeding gannets in Newfoundland (Montevecchi et al., 1980). Assuming an annual mortality of 80% (first-year birds; Nelson,1978a,b), there are approximately 7,440 non-breeding (≥5 years) individuals. With a hatching success of 86% (Montevecchi and Kirkham, unpubl. data), the total number of birds eating food during the season becomes about 34,000. It is assumed that non-breeders require on average about 750 kcal per day. Therefore, from the beginning of May to the end of September, about 1.7 x 10 9th kcal of fish are consumed (roughly 2.5 million mackerel). The annual mackerel catch

for 1979 in Newfoundland was 14.5 million kg, which according to Provincial Fisheries is at most, 33% of the potential catch. Since gannets eat some fish other than mackerel, they probably consume about 0.5% of the mackerel stocks in Newfoundland waters.

General Discussion

A question of primary interest regarding reproduction in Northern Gannets is: why do gannets have an altricial mode of development? The ganner's altricial mode of development is characterized by immaturity at hatching followed by a period of rapid growth. In contrast, precocial and semi-precocial species hatch with a greater portion of their eventual growth already complete but grow more slowly than altricials. These differences have been related to precocial species having eggs with larger yolks and greater lipid and protein concentrations (Ricklefs, 1977). The gannet's egg is similar to other altricial species in having a small yolk (15.5% fresh egg weight) and a very low dry matter content (yolk and albumen, 25.8%; Ricklefs and Montevecchi, 1979). The energy density (0.90 kcal/g) is the lowest known for any bird. The egg is about 3.5% of the females's weight (Heinroth, 1922; Nelson 1978a,b; Ricklefs and Montevecchi, 1979). Precocial chicks usually hatch with a yolk reserve which provides nutrition until they begin to feed for themselves. Embryonic development is far greater than in altricials, and tarsi and

thermoregulatory abilities are well developed at hatching. The initial investment of producing an egg for a precocial species is thus much higher compared to altricial species, and parental investment into nestlings is often less.

The largest birds (Struthio spp., Rhea spp.) are highly precocial and lay large numbers of eggs (e.g., Rhea americana - 13-20 eggs, Thomson, 1964). In order to produce large bodied precocial neonates, the egg must also be large (e.g., R. americana - 600g). The critical difference between the gannet and these large terrestrial birds is the nature of their food resources, and the methods of exploiting them. Gannets are pelagic (and opportunistic inshore) feeders, that often forage at great distances from the breeding colony. In order to exploit a pelagic feeding zone, gannets must be strong and efficient flyers. The long period required for wing development initially precludes self-feeding by nestlings, but eventually enables them to feed in offshore regions. Production of altricial young (characterized by rapid growth and high metabolic rate) is therefore the most efficient mode of development when young cannot exploit an ephemeral food resource requiring specialized skills.

This study investigated some of the interactions among the morphological, physiological and behavioural aspects of development in nestling gannets. It is during the first month, after hatching, that the most pronounced developmental

changes occur. Morphologically, the bill, legs and feet grow to between 80 and 100% of adult size. The rapid development of these body parts, combined with complete down cover (by 17 days), enable chicks to effectively thermoregulate and is correspondingly the period when parental brooding ceases. This pattern of growth, which is similar to other altricial species, is in part the result of an abundant and calorically rich food resource. Physiologically, during the first month, metabolism declines to adult levels, possibly indicating a decrease in energy expenditure (i.e., maturity of most body parts, and endothermic capacity). All these components affect the rate of development and represent an integrated reproductive strategy adapted to existing cellular constraints and the physical environment.

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APPENDIX A

History and Distribution

The gannet has a remarkable and well documented history. The late Leslie Tuck wrote a number of unpublished historical and distributional accounts of the extinct and extant Canadian gannetries, which provided the impetus for the writing of this brief historical sketch.

Cunninghan (1866) notes that the first mention of the gannet in the literature was around 975 A.D., when the growing colony of Bass Rock, Scotland is mentioned. Since then, the gannet has found its way into numerous historical and fictional works, including the epic poem "Beowulf" (Gurney, 1913). Many ornithologists have been inspired to write comprehensive accounts of this, the largest bird of northern coasts and seas. Since Gurney's popular account was published, it was not until recently that the gannet's biology was revised along with the other family members (Nelson, 1978a,b). Nelson (p.13, 1978a) writes of the intentions of the late James Fisher to write a monograph on the gannet, a goal never achieved. Nelson's works are the culmination of two decades of investigative study into sulid behaviour and biology.

North American gannetries were first documented by Jacques Cartier in 1534 (old calendar) at Funk Island (Biggar, 1924). Cartier's encounter with the gannets provides an amusing but accurate description: "There were

other white ones [gannets] larger still that keep apart from the rest in a portion of the island, and are very ugly to attack; for they bite like dogs." Cartier and his men landed on Funk Island to secure fresh meat after their long trans-Atlantic voyage. They found large numbers of the flightless and now extinct Great Auk (Pinguinis impennis) breeding there, which they found to be easy prey.

A world-wide survey of gannetries was conducted in 1939 by Fisher and Vevers (1944). Nettleship (1976) subsequently reported his census for North American gannetries, and Nelson (1978b) updated the estimated total world population numbers. There have been a few new counts (Montevecchi et al., 1980) since the Nettleship and Nelson publications. The population trends for North American colonies up to the most recent counts are summarized (Appendices B-F). From 1819 until the present, it has been estimated that the total number of breeding gannets in North America has declined from about 170,620 to 32,046 pairs. The Bird Rocks were possibly the largest gannetry in the world around the early 1800's (Nelson, 1978a). The decline is due primarily to an enormous reduction in the gannets breeding at the Bird Rocks in the Magdalen Islands, Quebec (Appendix B). The main reasons for the reduction at Bird Rock were: 1) the erosion of cliffs which are made up of red sandstone; 2) the exploitation of the birds by local fishermen (Bent, 1908); and 3) the erection of a lighthouse in 1869 which reduced

the number of summit nesters by 50,000 pairs in 20 years (Lucas, 1888).

The gannetry at Funk Island was present when Cartier visited there in 1534 and again in 1535 (Appendix C). By 1841, the colony had already become locally extinct, presumably shortly after the extinction of the Great Auks. Again, the gannet suffered persecution by the exploits of man. However, the colony was re-established in 1936 with seven breeding pairs (Gilliard, 1937). Today, Funk Island is protected as a sanctuary and the colony is expanding.

The gannets at Cape St.Mary's underwent a large population increase between 1880 and 1910 (Appendix D). Since Wynne-Edwards (1935) visited the stack at the Cape in 1934, the colony size has remained fairly stable and appears filled to capacity. Wynne-Edwards also mentioned the exploitation of the gannets by local fisherman, which likely discouraged the brief attempts at nesting on the mainland about 20 m away.

In 1941, Peters (1942) described the Baccalieu Island gannetry which somehow had been overlooked by ornithologists for over a 100 years (Templeman, 1945). There appears to be room for expansion in this colony, since L.M.Tuck in 1960 estimated 900 nesting pairs (Appendix E). This colony remains as the only gannetry in North America which is not protected under the Federal Migratory Bird Sanctuary Act.

There are three extinct gannetries in North America

(Appendix F). Perroquet Island, Quebec discovered in 1819 became extinct by 1889, the year after a lighthouse was erected. The Yarmouth colony in New Brunswick had 400 pairs in 1819 and by 1900 the colony had disappeared. The reasons for the extinction are unknown. The Grand Manan gannetry, New Brunswick, became extinct around 1870, almost 40 years after the erection of a lighthouse. The affects of human disturbance on gannets and other insular breeding colonial seabirds is usually devastating. However, the Bird Rock colony is still thriving even in face of the major disturbances of almost a century ago.

The world population numbers declined from 1819 (170,620 pairs) to 1894 (52,900 pairs; Fisher and Vevers, 1944). The decline was primarily the result of the near disappearance of the Bird Rocks colony. World numbers had increased slightly by 1939 (82,755 pairs) and then dramatically up to 1976 (213,000 pairs). Even at present day numbers, an estimate of 500,000 Northern Gannets (Nelson, 1978a) means they are the least abundant of the North Atlantic seabird species.

The six extant gannet colonies (three in Quebec and three in Newfoundland), contain several other seabird species. Many of the species are found in larger numbers than the gannets and include: Common and Thick-billed Murres (Uria aalge, U. lomvia), Northern Puffins (Fratercula arctica), Razorbill Auks (Alca torda), Black-legged

Kittiwakes (*Rissa tridactyla*) and two large gulls (*Larus argentatus*, *L. marinus*). The continued success of these breeding colonies rests in proper management (e.g., Jarvis, 1970) of associated human activities such as light stations and fishery quotas.

Appendix B. Census estimates of the number of pairs of Northern Gannets at Bird Rocks, Magdalen Islands, Quebec

Census year	Count (pairs)	Source
1534	(breeding)	J.Cartier (Biggar,1924)
1833	112,500	Audubon (1840-44)
1860	75,000	Bryant (1861)
1864	65,000	Fisher & Veyers (1944)
1872	27,500	Maynard (1896)
1881	25,000	Brewster (1883)
1887	5,000	Lucas (1888)
1898	1,000	Chapman (1898; in Tuck,1969)
1904	1,500	A.C.Bent (Gurney,1918)
1932	500	Fisher & Vevers (1944)
1934	1,250	A.O.Gross (in Tuck,1969)
1969	3,353	S.M.Temple (in Tuck,1969)
1973	5,331	Nettleship (1976)

Appendix C. Census estimates of the number of pairs of Northern Gannets at Funk Island, Newfoundland

Census year	Count (pairs)	Source
1534	(breeding)	J.Cartier (Biggar, 1924)
1887	0	Lucas (1888)
1934	0	Wynne-Edwards (1935)
1936	7	Gilliard (1937)
1945	200	Peters & Burleigh (1951)
1951	500	L.M.Tuck[1]
1952	600	L.M.Tuck[1]
1956	1,204	L.M.Tuck & D.H.Pimlott[1]
1959	2,768	L.M.Tuck & J.Fisher[1]
1967	2,960	L.M.Tuck & H.Boyd[1]
1969	2,796	J.Learning & J.Miller[1]
1972	4,000 (approx.)	Nettleship (1976)
1978	3,871	Montevecchi et al. (1980)

[1] from Tuck (unpubl. ms: 6).

Appendix D. Census estimates of the number of pairs of Northern Gannets at Cape St. Mary's, Newfoundland

Census year	Count (pairs)	Source
1879	3	Fisher & Vevers (1944)
1883	9	" "
1889	26	" "
1894	66	" "
1899	160	" "
1904	400	" "
1909	1,000	" "
1914	2,100	" "
1919	2,600	" "
1924	3,200	" "
1934	4,000	Wynne-Edwards (1935)
1939	4,394	Davies & Keynes (1948)
1942	5,000	Peters & Burleigh (1951)
1964	4,000	Seamans (1964)
1972	5,260	Nettleship (1976)
1977	4,866	Montevecchi et al.(1980)

Appendix E. Census estimates of the number of pairs of Northern Gannets at Baccalieu Island, Newfoundland

Census year	Count (pairs)	Source
1904	1	Fisher & Vevers (1944)
1909	3	" "
1914	5	" "
1919	11	" "
1924	21	" "
1934	79	" "
1939	150	" "
1941	200	Peters (1942)
1952	7-800	L.M.Tuck[1]
1953	7-800	D.E.Sergeant[1]
1959	208	R.T.Peterson[1]
1960	900	L.M.Tuck[1]
1969	351	J.Learning & J.Miller[1]
1973	673	Nettleship (1976)
1976-78	562	Montevecchi et al.(1980)

[1] from Tuck (unpubl. ms. b).

Appendix F. Population changes in North American gannetries

Colony: discovery year (pairs)	--	present day (pairs)
Bird Rocks	1833 (112,500) --	1973 (5,331)
Bonaventure	1819 (1,500) --	1973 (17,281)
Gull-cliff Bay	1904 (1) --	1972 (135)
[1]Grand Manan	1819 (40) --	1869 (1)
[1]Yarmouth	1819 (150) --	1879 (2)
[1]Perroquet	1819 (400) --	1884 (20)
Cape St.Mary's	1879 (3) --	1977 (4,866)
Baccalieu	1909 (3) --	1978 (562)
Funk	1534 (?) --	1978 (3,871)
Total	1819 (114,590) --	1978 (32,046)

[1]extinct after last count